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THE UNIVERSITY OF KANSAS
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CATALOGUE OF THE TYPES IN THE SNOW ENTOMOLOGICAL MUSEUM PART VI (COLEOPTERA)

By

George W. Byers and Jay B. Karren

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Vol. XX—October 1, 1932.
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Vol. XXII—November 15, 1935.
Vol. XXIII—August 15, 1936.
Vol. XXIV—February 16, 1938.
Vol. XXV—July 10, 1939.
Vol. XXVI—November 27, 1940.
Vol. XXVII, Pt. I—Dec. 30, 1941.
Vol. XXVIII, Pt. I—May 15, 1942.
Pt. II—Nov. 12, 1942.
Vol. XXIX, Pt. I—July 15, 1943.
Pt. II—Oct. 15, 1943.
Vol. XXX, Pt. I—June 12, 1944.
Pt. II—June 15, 1945.
Vol. XXXI, Pt. I—May 1, 1946.
Pt. II—Nov. 1, 1947.
Vol. XXXII—Nov. 25, 1948.
Vol. XXXIII, Pt. I—April 20, 1949.
Pt. II—March 20, 1950.
Vol. XXXIV, Pt. I—Oct. 1, 1951.
Pt. II—Feb. 15, 1952.
Vol. XXXV, Pt. I—July 1, 1952.
Pt. II—Sept. 10, 1953.
Pt. III—Nov. 20, 1953.
Vol. XXXVI, Pt. I—June 1, 1954.
Pt. II—July 15, 1954.
Vol. XXXVII, Pt. I—Oct. 15, 1955.
Pt. II—June 29, 1956.
Vol. XXXVIII, Pt. I—Dec. 20, 1956.
Pt. II—March 2, 1958.
Vol. XXXIX—Nov. 18, 1958.
Vol. XL—April 20, 1960.
Vol. XLI—Dec. 23, 1960.
Vol. XLII—Dec. 29, 1961.
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VOL. XLVIII PAGES 1 TO 20 SEPTEMBER 30, 1968 No. 1

Catalogue of the Types in the Snow Entomological Museum Part VI (Coleoptera)[1]

GEORGE W. BYERS AND JAY B. KARREN

ABSTRACT

Types of 544 species and subspecies of Coleoptera are catalogued, with references to original descriptions (except for species represented by paratypes only), number and condition of specimens, and type numbers as recorded in the Catalogue of Types in the Snow Entomological Museum.

INTRODUCTION

There have been only a few coleopterists among either staff or students in the Department of Entomology at The University of Kansas, which accounts for the relatively small number of types representing the vast order Coleoptera in the Snow Entomological Museum. Though not himself a coleopterist, the Museum's founder, Professor Francis H. Snow, attracted the attention of virtually every student of the order, and at the same time greatly enlarged the Museum's holdings in Coleoptera and other groups, when in 1877 he discovered large numbers of the rare tiger beetle, *Amblycheila cylindriformis* Say (which at that time commanded a collector's price of $15 a pair), in western Kansas, and subsequently exchanged dozens of pairs of these prized cicindelids for vast numbers of other insect specimens.

In his historical account of the Department of Entomology, Hunter (1914, Univ. Kansas Sci. Bull., 8: 3-61) listed types of 12 species of Coleoptera, representing the Museum's accumulation during its first 44 years. The present list includes 544 species and subspecies, indicating a substantial increase in coleopterological activity in the Museum during its second half century.

1. Contribution No. 1277 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

Students of Coleoptera directly associated with the Museum have included William J. Brown (specialist in Chrysomelidae), Milton W. Sanderson (Scarabaeidae and Elmidae), Stephen L. Wood (Scolytidae), Lyman S. Henderson (Curculionidae), Wilbur R. Enns (Meloidae) and Warwick Benedict. A few of the types catalogued below were received in exchange, while a larger number represent species described at least in part from specimens in the Snow Museum by coleopterists elsewhere.

In the catalogue of type specimens that follows, the families are arranged alphabetically, and beneath each family heading the genera and species are also arranged alphabetically, in two lists. The first list includes species represented by holotypes, allotypes, syntypes, lectotypes and neotypes, as well as paratypes if these are also present. For each species in this list, the reference to the original description is given, and, where applicable, references are given for designation of lectotypes and neotypes. The second list includes species represented in the Snow Museum by paratypes only and omits literature references. At the end of each entry, there appears the type number of the species from the Catalogue of Types in the Snow Entomological Museum.

Types of secondary status, such as metatypes, homotypes and plesiotypes, have not been included in this catalogue. Only those types representing taxonomically available species and actually present in the Museum as of 1967 are included. In some cases an original description indicated one or more types were deposited in the Snow Museum, whereas none—or a lesser number than that indicated—was actually found in the collection. On the other hand, an author may have stated that certain types were deposited elsewhere, while in fact they were placed in the Snow Museum. No attempt has been made to correct these inconsistencies.

Only the original combinations of generic and specific names have been used for each species, as we consider it impracticable to attempt to give the current generic assignment of those valid species that have been placed in different genera or the current specific name of those species now judged to be junior synonyms.

Specialists in Coleoptera seem to be little concerned about whether their specimens are male or female, and often—especially in the older descriptions —the sex of even the holotype is not stated. Perhaps this reflects a general similarity of the sexes in beetles, or a disinclination among coleopterists to be bothered with dissections. When the author of a species indicated the sex of the types, we have generally accepted his opinion as correct. Where this datum is lacking for types other than paratypes, we have offered our own opinion. Since coleopterists themselves have been satisfied to do without this information, we trust we shall be forgiven for not otherwise undertaking to supply it, here.

ACKNOWLEDGMENTS

We acknowledge with thanks the financial support provided by a grant from the General Research Fund of the University of Kansas, making possible the completion of this catalogue. We also wish to thank those who assisted us in the typing and other aspects of preparation of the catalogue.

Suborder ADEPHAGA

Carabidae

Harpalus (Pseudophonus) hatchi Ball & Anderson, 1962. The Taxonomy and Speciation of *Pseudophonus*: 41. ♂ holotype, ♀ allotype, 1 ♂ paratype. 6478.
Rhadine longicollis Benedict, 1927. Pan-Pacific Ent., 4: 44-46. ♂ holotype, ♀ allotype, 27 paratypes. 1079.

Carabidae—Paratypes

Badister (Baudia) parviceps Ball, 1959. 2 paratypes. 5443.
Bembidion bryanti Carr, 1932. 1 paratype. 1775.
Dicaelus dilatatus sinuatus Ball, 1959. 2 paratypes. 5445.
Dicaelus laevipennis dicaeloides Ball, 1954. 1 paratype. 5444.
Rhadine ozarkensis Sanderson & Miller, 1941. 1 paratype. 3430.

Cicindelidae—Paratypes

Cicindela abdominalis floridana Cartwright, 1939. 1 paratype. 3295.
Cicindela alata Liljeblad, 1932. 1 ♂, 1 ♀ paratypes. 1773.
Cicindela arida Davis, 1928. 1 paratype. 1078.
Cicindela formosa fletcheri Criddle, 1925. 1 paratype. 280.
Cicindela macrocnema kino Cazier, 1954. 2 paratypes. 5397.
Cicindela nevadica olmosa Vaurie, 1951. 12 ♂, 9 ♀ paratypes. 6078.
Cicindela nigrocoerulea subtropica Vogt, 1949. 1 paratype. 4079.
Cicindela rockefelleri Cazier, 1954. 1 paratype. 350.
Cicindela sinaloae schrammeli Cazier, 1954. 1 paratype. 501.
Omus subcylindricus Nunenmacher, 1940. 1 paratype. 3416.
Cicindela theatina Rotger, 1944. 3 ♂, 1 ♀ paratypes. 3820.
Omus vanlooi Nunenmacher, 1940. 2 paratypes. 3417.

Dytiscidae—Paratypes

Agabus bryanti Carr, 1930. 1 paratype. 680.
Agabus colymbus Leech, 1938. 4 paratypes. 5466.
Bidessus rogersi Young, 1941. 1 paratype. 3293.
Copelatus caelatipennis princeps Young, 1963. 4 paratypes. 6481.
Hydrocanthus regius Young, 1953. 5 paratypes. 4986.
Hydrovatus inexpectatus Young, 1963. 1 paratype. 6479.
Hydrovatus platycornis Young, 1963. 2 paratypes. 6480.
Matus leechi Young, 1953. 2 paratypes. 4985.
Rhantus zimmermanni Wallis, 1933. 2 paratypes. 5465.

Gyrinidae—Paratypes

Gyrinus instabilis Fall, 1930. 32 ♂, ♀ paratypes. 681.

Haliplidae—Paratypes

Brychius hungerfordi Spangler, 1954. 4 paratypes. 5447.
Peltodytes bradleyi Young, 1961. 1 ♂, 1 ♀ paratypes. 5402.
Peltodytes dietrichi Young, 1961. 5 ♂, 6 ♀ paratypes. 5831.
Peltodytes dunavani Young, 1961. 5 ♂, 3 ♀ paratypess. 5401.

Noteridae—Paratypes

Hydrocanthus regius Young, 1953. 10 ♂, ♀ paratypes. 4986.

Suborder POLYPHAGA

Alleculidae

Hymenorus alienus Fall, 1931. Trans. Amer. Ent. Soc., 57: 217-218. ♀ holotype. 6231.

Alleculidae—Paratypes

Hymenorus disparatus Fall, 1931. 3 paratypes. 6232.
Hymenorus inutilis Fall, 1931. 2 paratypes. 6233.
Hymenorus irritus Fall, 1931. 29 paratypes. 6234.
Hymenorus papagonis Fall, 1931. 3 paratypes. 6235.
Hymenorus thoracicus Fall, 1931. 1 paratype. 5855.

Anobiidae—Paratypes

Tricorynus abdominalis White, 1965. 1 paratype. 6465.
Tricorynus arizonicus White, 1965. 1 paratype. 6466.
Tricorynus gibbulus pubescens White, 1965. 1 paratype. 6467.
Tricorynus imitans White, 1965. 1 paratype. 6468.
Tricorynus inflatus White, 1965. 1 ♀ paratype. 6469.
Tricorynus moderatus White, 1965. 3 paratypes. 6470.
Tricorynus vittatus White, 1965. 1 ♂, 2 ♀ paratypes. 6471.

Anthribidae—Paratypes

Brachytarsus annulatus Carr, 1930. 2 paratypes. 3098.
Brachytarsus franseria Barrett, 1931. 5 paratypes. 3226.

Buprestidae

Agrilus baboquivariae Fisher, 1928. U.S. Nat. Mus. Bull., 145: 184-186. ♂ allotype. 3176.
Agrilus benjamini Fisher, 1928. Bull. U.S. Nat. Mus., 145: 107-109. ♀ allotype. 156.
Agrilus snowi Fall, 1905. Canadian Ent., 37: 270-271. ♂ holotype. 181.
Aphanisticus affinis Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 41-42. 14 syntypes. 3796.

Aphanisticus agriloides Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 38. 17 syntypes. 3791.
Aphanisticus sumatrensis Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 40. 15 syntypes. 3798.
Aphanisticus tristis Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 38-39. 17 syntypes. 3797.
Chrysobothris beameri Knull, 1954. Ohio Jour. Sci., 54: 27-28. ♂ holotype. 5310.
Endelus coeruleus Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 46. 13 syntypes. 3793.
Endelus collaris Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 45-46. 8 syntypes. 3792.
Endelus elongatus Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 44-45. 8 syntypes. 3795.
Endelus modiglianii Kerremans, 1896. Ann. Mus. Genova, 16: 366. 10 ♂, ♀ syntypes. 3794.
Sambus aeneus Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 19-20. 7 syntypes. 3801.
Trachys congener Kerremans, 1900. Mem. Soc. Ent. Belgique, 7: 59-60. 2 syntypes. 3802.
Trachys gentilis Kerremans, 1894. Ann. Mus. Genova, 14: 540-541. 4 ♂, 4 ♀ syntypes. 3799.

Buprestidae—Paratypes

Acmaeodera adenostomae Cazier, 1938. 1 paratype. 3432.
Acmaeodera chisosensis Knull, 1952. 1 paratype. 4652.
Acmaeodera fisheri vermiculata Knull, 1947. 1 paratype. 3739.
Acmaeodera ligulata Cazier, 1940. 3 paratypes. 3434.
Acmaeodera parkeri Cazier, 1940. 1 paratype. 3435.
Acmaeodera robusta duboisi Cazier, 1938. 1 paratype. 3433.
Actenodes simi Fisher, 1940. 1 paratype. 3117.
Agrilus exsapindi Vogt, 1949. 2 paratypes. 4078.
Agrilus malvastri Fisher, 1928. 9 paratypes. 151.
Agrilus politus pseudocoryli Fisher, 1928. 5 paratypes. 171.
Agrilus viridescens Knull, 1935. 3 paratypes. 2232.
Chrysobothris sexfasciata Schaeffer, 1918. 1 ♂ paratype. 2262.
Paratyndaris acaciae Knull, 1937. 2 paratypes. 3243.
Paratyndaris albofasciata Knull, 1937. 2 paratypes. 3235.
Taphrocerus albodistinctus Knull, 1954. 2 paratypes. 5311.
Taphrocerus huachucanus Knull, 1944. 11 paratypes. 3248.

Cantharidae—Paratypes

Silis (Silis) emarginata Green, 1966. 1 ♂ paratype. 6500.
Silis (Silis) subtruncata Green, 1966. 1 ♂ paratype. 6501.

Cebrionidae—Paratypes

Cebrio knausi VanDyke, 1932. 1 paratype. 1106.

Cerambycidae

Aneflus (Protaneflus) minutivestis Chemsak & Linsley, 1963. Bull. Brooklyn Ent. Soc., 58: 85-86. ♀ allotype. 6484.

Austrophanes robustum Chemsak & Linsley, 1963. Jour. Kansas Ent. Soc., 36: 218-219. ♂ holotype. 6486.

Coleomethia mexicana Chemsak & Linsley, 1964. Pan-Pacific Ent., 40: 161. ♂ holotype. 6488.

Eumimetes sparsus fasciatus Brancsik, 1893. Naturw. Ver. Trencsener Komitäts Jahresheft, 15: 242-243. 1 ♂ syntype. 2027.

Hetoemis cinerea bimaculata Dillon & Dillon, 1947. ♂ holotype, ♀ allotype, 3 ♂, 3 ♀ paratypes. 3777.

Leptostylus yuccivorus Fall, 1907. Jour. N.Y. Ent. Soc., 15: 83-84. ♂ holotype. 1157.

Pseudaneflus puncticollis Chemsak & Linsley, 1963. Entomol. News, 74: 87-88. ♂ holotype. 6485.

Sternidius alpha coloradensis Dillon, 1956. Ann. Ent. Soc. Amer., 49: 216. ♀ allotype. 5384.

Sternidius alpha nigricans Dillon, 1956. Ann. Ent. Soc. Amer., 49: 216-217. ♀ holotype. 5383.

Xeranoplium ruficolle Chemsak & Linsley, 1963. Jour. Kansas Ent. Soc., 36: 225-226. ♂ holotype. 6487.

Cerambycidae—Paratypes

Aneflus prolixus insoletus Chemsak & Linsley, 1963. 5 ♂ paratypes. 6483.

Astylidius versutus downei Dillon, 1956. 1 paratype. 5387.

Lagocheirus stroheckeri stroheckeri Dillon, 1956. 1 paratype. 5389.

Leptostylus transversus dakotensis Dillon, 1956. 11 paratypes. 5386.

Leptostylus transversus dietrichi Dillon, 1956. 1 paratype. 5385.

Olenecamptus bilobus mindanaensis Dillon & Dillon, 1947. 1 ♂, 1 ♀ paratypes. 3778.

Chrysomelidae

Clythra gibber Fabricius, 1798. Suppl. Ent. System.: 112. ♂ neotype, Karren, 1966, Univ. Kansas Sci. Bull., 46: 655. 6464.

Exema byersi Karren, 1966. Univ. Kansas Sci. Bull., 46: 670-672. ♂ holotype, ♀ allotype, 10 ♂, 11 ♀ paratypes. 6462.

Exema mormona Karren, 1966. Univ. Kansas Sci. Bull., 46: 659-662. ♂ holotype, ♀ allotype, 1 ♂, 1 ♀ paratypes. 6463.

Metronia creola Sanderson & King, 1951. Jour. Kans. Ent. Soc., 24: 128. ♂ holotype. 5671.

Metronia turba Sanderson & King, 1951. Jour. Kans. Ent. Soc., 24: 126-128. ♂ holotype, ♀ allotype, 3 ♂, 2 ♀ paratypes. 5672.

Pachybrachys coloradensis Bowditch, 1909. Canadian Ent., 41: 242. 1 ♀ syntype. 149.

Pachybrachys discoideus Bowditch, 1909. Canadian Ent., 41: 239. ♀ holotype. 1164.

Pachybrachys jacobyi Bowditch, 1909. Canadian Ent., 41: 240-241. 1 ♂ syntype. 1158.
Pachybrachys notatus Bowditch, 1910. Canadian Ent., 42: 53-54. ♂ holotype. 1162.
Pachybrachys sanrita Bowditch, 1909. Canadian Ent., 41: 289. 1 ♂ syntype. 1163.
Pachybrachys snowi Bowditch, 1909. Canadian Ent., 41: 290. 1 ♀ syntype. 1161.

Chrysomelidae—Paratypes

Altica populi Brown, 1938. 2 paratypes. 5461.
Altica ribis Brown, 1946. 2 ♀ paratypes. 5460.
Calligrapha alni Schaeffer, 1928. 1 paratype. 1171.
Calligrapha alnicola Brown, 1945. 1 paratype. 5454.
Calligrapha amator Brown, 1945. 1 ♂, 1 ♀ paratypes. 5455.
Calligrapha amelia confluens Schaeffer, 1928. 2 paratypes. 1170.
Calligrapha ostryae Brown, 1945. 4 ♀ paratypes. 5456.
Calligrapha pruni Brown, 1945. 1 ♂, 1 ♀ paratypes. 5457.
Calligrapha tiliae Brown, 1945. 1 ♀ paratype. 5459.
Calligrapha virginea Brown, 1945. 2 paratypes. 5458.
Chrysomela alnicola alnicola Brown, 1956. 1 ♂, 1 ♀ paratypes. 6218.
Chrysomela alnicola interna Brown, 1956. 1 ♂, 1 ♀ paratypes. 6219.
Chrysomela alnicola littorea Brown, 1956. 1 ♀ paratype. 6220.
Chrysomela crotchi Brown, 1956. 1 ♂, 1 ♀ paratypes. 6221.
Chrysomela falsa Brown, 1956. 1 ♂, 1 ♀ paratypes. 6222.
Chrysomela hudsonica Brown, 1938. 2 ♂ paratypes. 5464.
Chrysomela invicta Brown, 1956. 1 ♀ paratype. 6223.
Chrysomela knabi Brown, 1956. 1 ♂, 3 ♀ paratypes. 6224.
Chrysomela laurentia Brown, 1956. 1 ♂, 3 ♀ paratypes. 6225.
Chrysomela semota Brown, 1956. 4 ♀ paratypes. 6226.
Chrysomela walshi Brown, 1956. 1 ♂, 1 ♀ paratypes. 6227.
Cryptocephalus snowi Schaeffer, 1933. 3 paratypes. 1166.
Cryptocephalus umbonatus Schaeffer, 1906. 1 paratype. 1165.
Entomoscelis americana Brown, 1942. 1 ♀ paratype. 5463.
Euphrytus parvicollis Schaeffer, 1933. 1 paratype. 1168.
Euphrytus snowi Schaeffer, 1933. 11 paratypes. 1167.
Exema elliptica Karren, 1966. 2 ♂, 2 ♀ paratypes. 6461.
Galerucella ribicolla confusa Brown, 1946. 2 paratypes. 5462.
Haltica betulae Schaeffer, 1924. 1 paratype. 1180.
Haltica canadensis Gentner, 1926. 1 paratype. 1177.
Haltica elongata Gentner, 1926. 1 paratype. 1178.
Haltica kalmiae viridana Schaeffer, 1932. 1 paratype. 1183.
Haltica liebecki Schaeffer, 1924. 1 paratype. 1179.
Lina obsoleta scriptoides Schaeffer, 1928. 1 paratype. 3714.
Monoxia inornata Blake, 1939. 62 ♂, and ♀ paratypes. 1885.
Monoxia puberula Blake, 1939. 2 paratypes. 1887.
Oedionychis lugens lamprocyannea Blake, 1927. 14 paratypes. 3580.
Phratora americana canadensis Brown, 1951. 2 ♀ paratypes. 1360.

Phratora frosti frosti Brown, 1951. 1 ♂, 1 ♀ paratypes. 1356.
Phratora purpurea kenaiensis Brown, 1952. 1 ♂, 1 ♀ paratypes. 1355.
Phratora purpurea novae-terrae Brown, 1951. 1 ♀ paratype. 1358.
Phratora purpurea purpurea Brown, 1951. 1 ♂, 1 ♀ paratypes. 1354.
Phyllodecta akliviki Carr, 1932. 2 paratypes. 1776.
Phyllotreta columbiana Chittenden, 1927. 1 paratype. 1182.
Trirhabda adela Blake, 1931. 14 paratypes. 1172.
Trirhabda borealis Blake, 1931. 12 paratypes. 1173.
Trirhabda borealis indigoptera Blake, 1931. 1 paratype. 1174.
Trirhabda pilosa Blake, 1931. 7 paratypes. 1175.
Trirhabda sericotrachyla Blake, 1931. 13 paratypes. 1176.
Xanthonia pinicola Schaeffer, 1933. 1 paratype. 1169.

Cleridae

Clerus bimaculatus Skinner, 1905. Ent. News, 16: 291-292. 1 ♂, 1 ♀ syntypes. 1099.
Cymatodera horni Wolcott, 1910. Field Mus. Nat. Hist., Zool. Ser., 7: 349. ♀ holotype. 4115.
Cymatodera snowi Wolcott, 1910. Field Mus. Nat. Hist., Zool. Ser., 7: 349. ♂ holotype, 1 paratype. 1096.
Cymatodera subsimilis Wolcott, 1910. Field Mus. Nat. Hist., Zool. Ser., 7: 343-344. 1 ♀ syntype. 1095.

Cleridae—Paratypes

Aulicus dentipes Schaeffer, 1921. 3 paratypes. 1100.

Coccinellidae—Paratypes

Hyperaspis acanthicola Chapin, 1966. 1 ♂, 1 ♀ paratypes. 6498.
Scymnus (Pullus) hortensis Wingo, 1952. 3 ♂, 6 ♀ paratypes. 3175.

Curculionidae

Listronotus blandus Henderson, 1939. Univ. Kans. Sci. Bull., 26: 282-284. ♂ holotype, ♀ allotype, 15 paratypes. 3318.
Lixus crassipunctatus Chittenden, 1930. Proc. U.S. Nat. Mus., 77: 9-10. ♂ holotype. 1772.
Rhynchaenus caudatus Say, 1824. Jour. Acad. Nat. Sci. Phila., 3: 311-312. ♂ neotype, ♀ neallotype, 5 neoparatypes, Henderson, 1939, Univ. Kans. Sci. Bull., 26: 234-243. 3320.

Curculionidae—Paratypes

Apion buchanani Kissinger, 1957. 1 ♂, 1 ♀ paratypes. 6230.
Apion sectator Kissinger, 1957. 1 ♂, 1 ♀ paratypes. 6229.
Apion (Trichapion) oriotes Kissinger, 1959. 4 ♂, 9 ♀ paratypes. 6228.
Calendra corona Vaurie, 1954. 1 paratype. 5396.
Cylindrocopturus medicatus Carr, 1929. 1 paratype. 640.
Isodacrys burkei Howden, 1961. 1 ♀ paratype. 6477.
Listroderes squamiger Say, 1831. 3 neoparatypes. 3335.

Listronotus blatchleyi Henderson, 1939. 3 paratypes. 3319.
Listronotus distinctus Henderson, 1939. 3 paratypes. 3323.
Listronotus impressus Van Dyke, 1929. 1 paratype. 644.
Listronotus ingens Henderson, 1939. 3 paratypes. 3325.
Listronotus insignis Henderson, 1939. 6 paratypes. 3326.
Listronotus leechi Sleeper, 1955. 1 paratype. 5453.
Listronotus manifestus Henderson, 1939. 2 paratypes. 3327.
Listronotus similis Henderson, 1939. 2 paratypes. 3333.
Lixus blakeae Chittenden, 1928. 4 paratypes. 1769.
Lixus pervestitus Chittenden, 1930. 3 paratypes. 1770.
Lixus tricristatus Chittenden, 1930. 1 paratype. 1771.
Tachypterellus consors cerasi List, 1932. 2 paratypes. 1945.
Tachypterellus quadrigibbus magnus List, 1932. 2 paratypes. 1944.
Trichalophus stefanssoni Leng, 1919. 1 paratype. 676.

Dermestidae—Paratypes

Trogoderma ballfinchae Beal, 1954. 1 ♂ paratype. 5156.
Trogoderma boron Beal, 1954. 3 paratypes. 5154.
Trogoderma grassmani Beal, 1954. 3 paratypes. 5157.
Trogoderma parabile Beal, 1954. 3 paratypes. 5155.
Trogoderma sternale maderae Beal, 1954. 1 paratype. 5158.

Dryopidae—Paratypes

Helichus fastigiatus Say, 1824. 6 neoparatypes. 4134.
Helichus musgravei Hinton, 1935. 6 paratypes. 677.
Helichus triangularis Musgrave, 1935. 5 paratypes. 4135.

Elateridae

Cardiophorus arizonicus Fall, 1905. Canadian Ent., 37: 270. ♂ holotype. 1107.
Melanotus beameri Quate, 1967. Proc. U.S. Nat. Mus., 121: 56. ♂ holotype, 25 ♂ paratypes. 6502.

Elateridae—Paratypes

Ludius aeripennis destructor Brown, 1935. 1 paratype. 2244.
Ludius funereus Brown, 1936. 1 paratype. 2249.
Ludius inutilis Brown, 1936. 1 paratype. 2248.
Ludius propola columbianus Brown, 1936. 1 paratype. 2246.
Ludius pudicus Brown, 1936. 1 paratype. 2247.
Ludius viduus Brown, 1936. 1 paratype. 2245.
Melanotus lanceatus Quate, 1967. 6 ♂ paratypes. 6503.

Elmidae

Elmis crenatus Say, 1824. Keating's Exped. to Source of St. Peters Riv., 2, Append.: 275. ♂ neotype, ♀ neallotype, 29 neoparatypes, Sanderson, 1938, Univ. Kansas Sci. Bull., 25: 667. 4141.
Stegoelmis hintoni Sanderson, 1953. Coleopt. Bull., 7: 34-35. ♂ holotype, ♀ allotype. 1365.

Stenelmis antennalis Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 695-696.
♀ allotype, 17 paratypes. 4136.
Stenelmis beameri Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 671-672.
♂ holotype, ♀ allotype, 146 ♂, ♀ paratypes. 4137.
Stenelmis concinna Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 674-675.
♂ holotype, ♀ allotype, 38 ♂, ♀ paratypes. 4139.
Stenelmis decorata Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 701-702.
♂ holotype, ♀ allotype, 73 ♂, ♀ paratypes. 4142.
Stenelmis douglasensis Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 685.
♂ holotype, ♀ allotype, 14 ♂, ♀ paratypes. 4143.
Stenelmis exigua Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 669-670.
♂ holotype, ♀ allotype. 4144.
Stenelmis exilis Sanderson, 1938. Univ. Kans. Sci. Bull., 25:680-681.
♀ holotype, 1 ♀ paratype. 4159.
Stenelmis geayi Grouvelle, 1908. Bull. Mus. Nat. Hist. Natur. Paris, 14: 181-182.
1 ♂, 1 ♀ syntypes. 4163.
Stenelmis grossa Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 686-688.
♂ holotype, ♀ allotype, 8 paratypes. 4147.
Stenelmis hungerfordi Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 690-691.
♂ holotype, ♀ allotype, 98 ♂, ♀ paratypes. 4149.
Stenelmis lateralis Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 672-673.
♂ holotype, ♀ allotype, 154 ♂, ♀ paratypes. 4150.
Stenelmis mera Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 682-684.
♂ holotype, ♀ allotype, 25 ♂, ♀ paratypes. 4152.
Stenelmis mirabilis Sanderson, 1938. Univ. Kans. Sci. Bul., 25: 693.
♂ holotype, ♀ allotype. 4153.
Stenelmis musgravei Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 698-699.
♂ holotype, ♀ allotype, 5 paratypes. 4154.
Stenelmis parva Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 688-689. ♀ allotype. 4156.
Stenelmis sexlineata Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 663-665.
♂ holotype, ♀ allotype, 46 ♂, ♀ paratypes. 4158.
Stenelmis tarsalis Sanderson, 1938. Univ. Kans. Sci. Bull., 25: 675-677.
♂ holotype, ♀ allotype, 65 ♂, ♀ paratypes. 4160.

Elmidae—Paratypes

Cylloepus danforthi Musgrave, 1935. 2 paratypes. 4124.
Cylloepus spinipes Hinton, 1934. 4 paratypes. 4125.
Elsianus sandersoni Hinton, 1936. 1 paratype. 4130.
Helmis dietrichi Musgrave, 1933. 2 paratypes. 4161.
Helmis haitiana Darlington, 1936. 1 paratype. 4131.
Helmis koebelei Martin, 1927. 2 paratypes. 4169.
Helmis lahottensis Darlington, 1936. 1 paratype. 4133.
Helmis pusilla apta Musgrave, 1933. 1 paratype. 4177.
Helmis pusilla lödingi Musgrave, 1933. 1 paratype. 4178.
Helmis pusilla perdita Musgrave, 1933. 1 paratype. 4179.

Helmis solutus Brown, 1933. 2 paratypes. 4132.
Helmis thermarum Darlington, 1928. 2 paratypes. 4181.
Lara avara amplipennis Darlington, 1929. 4 paratypes. 4138.
Limnius cryophilus Musgrave, 1932. 1 paratype. 4166.
Limnius subarcticus Brown, 1930. 1 paratype. 4172.
Limnius ungulatus Hinton, 1934. 6 paratypes. 4164.
Neoelmis gracilis Musgrave, 1935. 2 paratypes. 4148.
Phanocerus helmoides Darlington, 1936. 1 paratype. 4151.
Stenelmis calida Chandler, 1949. 9 paratypes. 4123.
Stenelmis calida moapa LaRivers, 1941. 13 paratypes. 4157.
Stenelmis convexula Sanderson, 1938. 8 paratypes. 4140.
Stenelmis fuscata Blatchley, 1925. 1 paratype. 4162.
Stenelmis nevermanni Hinton, 1936. 2 paratypes. 1363.
Stenelmis nubifer Fall, 1901. 1 paratype. 4155.

Erotylidae

Triplax errans Boyle, 1956. Bull. Amer. Mus. Nat. Hist., 110: 110. ♂ holotype. 5647.

Erotylidae—Paratypes

Dacne cyclochilus Boyle, 1954. 2 paratypes. 5446.
Dacne (Xenodacne) pubescens Boyle, 1956. 2 paratypes. 5648.

Eucnemidae—Paratypes

Melasis tsugae Hopping, 1926. 1 paratype. 1108.

Heteroceridae—Paratypes

Heterocerus glicki Pacheco, 1963. 15 paratypes. 3162.
Heterocerus intermuralis Pacheco, 1963. 15 paratypes. 3166.
Heterocerus stankerus Pacheco, 1963. 15 paratypes. 3168.
Neoheterocerus sandersoni Pacheco, 1964. 1 ♂, 1 ♀ paratypes. 6495.
Peditatus texanus Pacheco, 1964. 1 ♂ paratype. 6494.

Histeridae—Paratypes

Geomysaprinus goffi Ross, 1940. 2 ♂, 2 ♀ paratypes. 3294.

Hydrophilidae—Paratypes

Tropisternus mexicanus viridis Young & Spangler, 1956. 1 ♂, 1 ♀ paratypes. 2025.

Lampyridae

Photinus australis Green, 1956. Proc. Calif. Acad. Sci., 28: 584-586. ♂ holotype, 3 paratypes. 5180.

Lampyridae—Paratypes

Photinus brimleyi Green, 1956. 2 paratypes. 5309.
Photinus consimilis Green, 1956. 2 paratypes. 5312.
Photinus cookii Green, 1956. 1 paratype. 5313.
Photinus curtatus Green, 1956. 2 paratypes. 5178.

Photinus frosti Green, 1956. 1 paratype. 4998.
Pyractomena floridana Green, 1958. 1 paratype. 2011.
Pyractomena marginalis Green, 1958. 1 paratype. 2012.
Photinus texanus Green, 1956. 1 paratype. 5179.
Pyropyga alticola Green, 1961. 1 paratype. 5014.
Pyropyga modesta Green, 1961. 11 paratypes. 5009.

Lycidae

Caloptognatha beameri Green, 1954. Coleop. Bull. 8: 56-57. ♂ holotype. 5825.

Malachiidae—Paratypes

Listrus fulvipilosus Blaisdell, 1921. 1 paratype. 3415.
Malachius californicus Barrett, 1931. 2 paratypes. 3178.
Microlipus falli Hopping, 1925. 1 paratype. 1086.
Trichochrous benedicti Blaisdell, 1924. 1 paratype. 1089.
Trichochrous nevadensis Blaisdell, 1942. 2 paratypes. 1113.
Trichochrous pratensis Blaisdell, 1923. 1 paratype. 1090.
Trichochrous quadrinotatus Blaisdell, 1930. 14 paratypes. 1088.

Melandryidae—Paratypes

Microscapha californica Barrett, 1928. 6 paratypes. 5021.

Meloidae

Epicauta ennsi Werner, 1957. Proc. Ent. Soc. Washington, 59: 97-98. ♂ holotype, 1 paratype. 5049.
Hornia gigantea Wellman, 1911. Ent. News, 22: 16-17. ♂ holotype, ♀ allotype, 3 paratypes. 1104.
Lytta reticulata Say, 1824. Jour. Acad. Nat. Sci. Phila., 3: 305. ♂ neotype, Selander, 1960, Ill. Biol. Monogr., No. 28: 104. 2018.
Lytta sphaericollis Say, 1824. Jour. Acad. Nat. Sci. Phila., 3: 299-300. ♂ neotype, Selander, 1955, Amer. Mus. Novit., No. 1730: 20. 2019.
Zonitus sulcicollis Blatchley, 1910. Coleoptera of Indiana: 1357. ♀ neallotype, Enns, 1956, Univ. Kansas Sci. Bull., 37: 806. 3177.

Meloidae—Paratypes

Calospasta wenzeli Skinner, 1904. 1 paratype. 1103.
Epicauta tenebrosa Werner, 1949. 1 ♂, 1 ♀ paratypes. 4072.
Hornia boharti Linsley, 1942. 1 paratype. 5022.
Hornia minutipennis occidentalis Linsley, 1942. 1 ♂, 1 ♀ paratypes. 3123.
Leonidea anthophorae Mickel, 1928. 1 paratype. 1105.
Lytta biguttata pallens Selander, 1956. 10 paratypes. 5403.

Mordellidae—Paratypes

Larisia nigricolor Liljeblad, 1945. 2 paratypes. 1102.

Nitidulidae—Paratypes

Cateretes (Cateretes) sissus Parsons, 1943. 2 paratypes. 3444.
Epuraea populi Dodge, 1939. 1 paratype. 2881.

Lobiopa falli Parsons, 1938. 6 paratypes. 2483.
Thalycra acuta Howden, 1961. 1 ♀ paratype. 5958.
Thalycra dentata Howden, 1961. 1 ♂, 1 ♀ paratypes. 5961.
Thalycra keltoni Howden, 1961. 1 ♂, 1 ♀ paratypes. 5960.
Thalycra mixta Howden, 1961. 1 ♀ paratype. 5955.
Thalycra monticola Howden, 1961. 1 ♀ paratype. 5956.
Thalycra parsonsi Howden, 1961. 1 ♂, 1 ♀ paratypes. 5957.
Thalycra sinuata Howden, 1961. 2 ♂, 1 ♀ paratypes. 5959.

Ostomidae—Paratypes

Temnochila sonorana Barrett, 1932. 2 paratypes. 2383.

Pedilidae

Duboisius benedicti Abdullah, 1961. Coleopterist's Bull., 15: 98-99. ♂ holotype. 3171.
Duboisius emarginatus Abdullah, 1961. Coleopterist's Bull., 15: 103. ♀ holotype. 3173.

Pedilidae—Paratypes

Duboisius howdeni Abdullah, 1961. 1 paratype. 3174.
Pedilus medius Abdullah, 1964. 1 paratype. 6489.
Qadrius quietus Abdullah, 1964. 1 paratype. 3167.

Pselaphidae

Arthmius (Arthmius) morsus Fletcher, 1932. Canadian Ent., 64: 33-34. ♂ holotype. 1800.
Batrisodes beameri Park, 1956. Jour. Tennessee Acad. Sci., 31: 66-67. ♂ holotype. 5601.
Decarthron diversum Park, 1958. Jour. Tennessee Acad. Sci., 33: 63. ♂ holotype, 2 ♀ paratypes. 5822.
Reichenbachia hardyi Park, 1956. Jour. Tennessee Acad. Sci., 31: 89-91. ♂ holotype, 1 ♀ paratype. 5602.
Reichenbachia ignobilis Fletcher, 1932. Canadian Ent., 64: 32. ♂ holotype. 1799.
Reichenbachia snowi Fletcher, 1932. Canadian Ent., 64: 31-32. ♂ holotype. 1798.

Ptinidae—Paratypes

Ptinus ocellus Brown, 1929. 2 paratypes. 1124.

Pyrochroidae

Dendroides pacificus Barrett, 1932. Pan-Pacific Ent., 8: 171. ♂ holotype. 2382.

Scarabaeidae

Aphodius anomaliceps Brown, 1929. Canadian Ent., 61: 207-208. ♂ holotype, ♀ allotype, 1 paratype. 1140.
Aphodius tuberosus Barrett, 1932. Canadian Ent., 64: 240. ♀ allotype, 51 paratypes. 3181.
Benedictia pilosa Sanderson, 1939. Jour. Kans. Ent. Soc., 12: 2-4. ♂ holotype. 2592.

Cremastocheilus (Macropodina) beameri Cazier, 1940. Bull. Brooklyn Ent. Soc., 35: 126-127. ♂ holotype. 3443.
Dichelonyx arizonica Barrett, 1933. Canadian Ent., 65: 132. ♂ holotype, ♀ allotype. 2446.
Euphoria (Errhipis) herbacea occidentalis Knaus, 1916. Bull. Brooklyn Ent. Soc., 11: 84. ♂ holotype, ♀ allotype. 1156.
Hoplia oregona deserticola Boyer, 1940. Microentomology, 5: 20-21. ♀ allotype, 50 ♂, ♀ paratypes. 2479.
Leptohoplia testaceipennis Saylor, 1935. Pan-Pacific Ent., 11: 133-134. ♀ allotype. 693.
Listrochelus duncani Barrett, 1933. Canadian Ent., 65: 129-130. ♂ holotype. 2590.
Phobetus leachi Barrett, 1935. Canadian Ent., 67: 51. ♂ holotype, 10 ♂ paratypes. 718.
Phobetus mojavus Barrett, 1933. Canadian Ent., 65: 130-132. ♂ holotype, ♀ allotype, 2 paratypes. 721.
Phoebetus sloopi Barrett, 1933. Canadian Ent., 65: 130. ♂ holotype, ♀ allotype, 62 ♂, ♀ paratypes. 722.
Phyllophaga beameri Sanderson, 1958. Jour. Kans. Ent. Soc., 31: 171-172. ♂ holotype. 5791.
Phyllophaga howei Sanderson, 1937. Jour. Kans. Ent. Soc., 10: 17-18. ♂ holotype. 2277.
Phyllophaga inflexa Barrett, 1935. Canadian Ent., 67: 49. ♂ holotype, ♀ allotype, 28 paratypes. 3431.
Phyllophaga inopia Sanderson, 1942. Jour. Kans. Ent. Soc., 15: 51-53. ♂ holotype, ♀ allotype, 8 paratypes. 3345.
Phyllophaga panorpa Sanderson, 1950. Jour. Kans. Ent. Soc., 23: 91-92. ♂ holotype, ♀ allotype, 1 paratype. 4265.
Phyllophaga perita Sanderson, 1937. Jour. Kans. Ent. Soc., 10: 14-15. ♂ holotype. 2279.
Phyllophaga (Phytalus) omani Sanderson, 1937. Jour. Kans. Ent. Soc., 10: 66-68. ♂ holotype, ♀ allotype. 1080.
Phyllophaga (Listrochelus) snowi Saylor, 1940. Proc. U.S. Nat. Mus., 89: 114. ♂ holotype. 3179.
Phyllophaga texana Sanderson, 1937. Jour. Kans. Ent. Soc., 10: 16-17. ♂ holotype. 2278.
Serica catalina Dawson, 1947. Jour. N.Y. Ent. Soc., 55: 234-235. ♂ holotype, 8 ♂, 8 ♀ paratypes. 3776.

Scarabaeidae—Paratypes

Acoma arizonica Brown, 1929. 2 paratypes. 1149.
Acoma minuta Cazier, 1953. 1 paratype. 4981.
Aegialia conferta punctata Brown, 1931. 1 paratype. 2377.
Aegialia criddlei Brown, 1931. 1 paratype. 2379.
Aegialia (Leptaegialia) browni Saylor, 1934. 1 paratype. 2376.
Aegialia opaca Brown, 1931. 1 paratype. 2378.

Anomala kansana Hayes & McCollock, 1924. 4 paratypes. 687.
Aphodius albertanus Brown, 1928. 1 ♀ paratype. 2411.
Aphodius brimleyi Cartwright, 1939. 2 paratypes. 2878.
Aphodius bryanti Brown, 1929. 2 paratypes. 1138.
Aphodius cavidomus Brown, 1927. 6 paratypes. 1131.
Aphodius corruptor Brown, 1929. 2 ♀ paratypes. 1130.
Aphodius cynomysi Brown, 1927. 3 paratypes. 1129.
Aphodius davisi Fall, 1930. 2 paratypes. 1141.
Aphodius dentigerulus Brown, 1929. 4 paratypes. 1137.
Aphodius geomysi Cartwright, 1939. 2 paratypes. 2879.
Aphodius goffi Cartwright, 1939. 2 paratypes. 2877.
Aphodius hamatus garmani Brown, 1929. 2 paratypes. 1128.
Aphodius odocoilis Robinson, 1939. 1 paratype. 3122.
Aphodius oklahomensis Brown, 1928. 1 paratype. 2110.
Aphodius peculiosus auvemeanus Brown, 1928. 2 paratypes. 2424.
Aphodius pingellus Brown, 1929. 2 paratypes. 1139.
Aphodius punctissimus Brown, 1928. 1 ♂, 2 ♀ paratypes. 1133.
Aphodius rossi Cartwright, 1944. 2 paratypes. 3829.
Aphodius sepultus Cartwright, 1944. 4 paratypes. 3830.
Aphodius snowi Brown, 1929. 1 paratype. 1136.
Aphodius socialis Brown, 1928. 2 paratypes. 1135.
Aphodius sparsus sheldoni Barrett, 1932. 2 paratypes. 2425.
Aphodius talpoidesi Brown, 1928. 3 paratypes. 1134.
Aphodius thomomysi Brown, 1928. 6 paratypes. 1132.
Aphodius vandykei Barrett, 1931. 7 paratypes. 1142.
Ataenius miamii Cartwright, 1934. 2 paratypes. 2374.
Bolbelasmus variabilis Howden, 1964. 4 ♂, 6 ♀ paratypes. 6490.
Bolbocerastes imperialis Cartwright, 1953. 2 paratypes. 5173.
Bolbocerastes imperialis kansanus Cartwright, 1953. 12 paratypes. 5174.
Bolbocerastes regalis Cartwright, 1953. 7 paratypes. 5172.
Bolbocerosoma confusum Brown, 1928. 1 paratype. 689.
Canthon bispinatus Robinson, 1941. 1 paratype. 3118.
Coenonycha ampla Cazier, 1943. 1 ♂, 1 ♀ paratypes. 3440.
Coenonycha barri Cazier, 1943. 2 paratypes. 3441.
Coenonycha fusca McClay, 1943. 2 paratypes. 3805.
Coenonycha hageni Cazier, 1943. 1 ♂, 1 ♀ paratypes. 3439.
Coenonycha scotti McClay, 1943. 5 paratypes. 3445.
Coenonycha testacea Cazier, 1937. 10 paratypes. 3488.
Coenonycha tingi Cazier, 1937. 10 paratypes. 3437.
Copris hintoni Saylor, 1933. 1 ♂, 1 ♀ paratypes. 2013.
Cotinis (Cotinis) fuscopicea Goodrich, 1966. 1 ♂, 1 ♀ paratypes. 6499.
Cyclocephala atricolor Chapin, 1932. 1 paratype. 4549.
Cyclocephala cubana Chapin, 1932. 6 paratypes. 4548.
Dialytes criddlei Brown, 1929. 1 paratype. 2375.
Dichelonyx vandykei Saylor, 1932. 1 paratype. 2250.
Diplotaxis circulans Vaurie, 1960. 1 ♂ paratype. 4640.

Diplotaxis impressifrons Cazier, 1940. 2 paratypes. 686.
Eucanthus impressus Howden, 1964. 1 ♂, 2 ♀ paratypes. 6491.
Eucanthus lazarus subtropicus Howden, 1955. 1 paratype. 4982.
Eucanthus mexicanus Howden, 1964. 1 ♀ paratype. 6492.
Glaresis knausi Brown, 1928. 14 paratypes. 1159.
Gymnopyga hirsuta Cazier, 1939. 1 paratype. 3442.
Listrochelus plenus Fall, 1932. 2 paratypes. 2598.
Neoathyreus quadridentatus Howden, 1964. 1 ♂ paratype. 6493.
Ochodaeus kansanus Fall, 1909. 4 paratypes. 1143.
Odontaeus darlingtoni Wallis, 1928. 2 paratypes. 1145.
Odontaeus falli Wallis, 1928. 3 paratypes. 1144.
Odontaeus liebecki Wallis, 1928. 1 paratype. 1147.
Odontaeus simi Wallis, 1928. 2 paratypes. 1146.
Odontaeus thoracicornis Wallis, 1928. 1 paratype. 1148.
Onthophagus browni Howden & Cartwright, 1963. 1 ♂, 1 ♀ paratypes. 6482.
Onthophagus cynomysi Brown, 1927. 1 paratype. 1125.
Onthophagus medorensis Brown, 1929. 6 paratypes. 1126.
Onthophagus oklahomensis Brown, 1927. 6 paratypes. 1127.
Phobetus ciliatus Barrett, 1935. 16 ♂ paratypes. 709.
Phobetus palpalis Saylor, 1936. 3 paratypes. 2252.
Phyllophaga aurea Luginbill & Painter, 1941. 2 paratypes. 3346.
Phyllophaga (Listrochelus) arizona Saylor, 1940. 1 paratype. 2588.
Phyllophaga (Listrochelus) chapini Saylor, 1940. 2 paratypes. 2585.
Phyllophaga (Listrochelus) granti Saylor, 1940. 1 paratype. 2586.
Phyllophaga (Listrochelus) huachuca Saylor, 1940. 2 paratypes. 2589.
Phyllophaga (Listrochelus) texensis Saylor, 1940. 3 paratypes. 2587.
Phyllophaga (Listrochelus) wickhami Saylor, 1940. 1 paratype. 2584.
Phyllophaga lodingi Sanderson, 1939. 1 paratype. 2593.
Phyllophaga plena Reinhard, 1939. 18 paratypes. 1949.
Phyllophaga pleroma Reinhard, 1940. 18 paratypes. 1949.
Phyllophaga riviera Reinhard, 1950. 8 paratypes. 4286.
Phyllophaga rubricosa Reinhard, 1939. 21 paratypes. 2599.
Phyllophaga sacoma Reinhard, 1939. 6 paratypes. 2600.
Phyllophaga sequoiana Saylor, 1936. 2 paratypes. 1986.
Phyllophaga sodalis Reinhard, 1940. 4 paratypes. 3429.
Phyllophaga sylvatica Sanderson, 1942. 1 paratype. 3428.
Phyllophaga tecta Cartwright, 1944. 2 paratypes. 3446.
Phyllophaga tristis amplicornis Reinhard, 1939. 12 paratypes. 2595.
Phyllophaga tristis apicata Reinhard, 1939. 4 paratypes. 2594.
Phyllophaga youngi Cartwright, 1935. 4 paratypes. 2120.
Phyllophaga zavalana Reinhard, 1946. 14 paratypes. 3647.
Pleurophorus atlanticus Cartwright, 1948. 1 paratype. 3831.
Pleurophorus longulus Cartwright, 1948. 1 paratype. 3832.
Podolasia pilosa Howden, 1954. 18 paratypes. 4980.
Psammodius mcclayi Cartwright, 1955. 10 paratypes. 5175.
Serica acicula Dawson, 1932. 10 paratypes. 2434.

Serica atratula monita Dawson, 1947. 2 ♂, 2 ♀ paratypes. 3774.
Serica chaetosoma Dawson, 1932. 1 ♂, 1 ♀ paratypes. 2435.
Serica concinna Dawson, 1947. 2 ♂, 2 ♀ paratypes. 3772.
Serica contorta Dawson, 1947. 2 ♂, 2 ♀ paratypes. 3775.
Serica imitans Chapin, 1931. 10 paratypes. 2433.
Serica lecontei Dawson, 1921. 1 paratype. 1153.
Serica pavonia Dawson, 1932. 2 ♂, 1 ♀ paratypes. 2123.
Serica perigonia Dawson, 1920. 1 ♀ paratype. 1152.
Serica pruinosa Saylor, 1935. 2 paratypes. 2251.
Serica satrapa Dawson, 1947. 2 ♂, 2 ♀ paratypes. 3773.
Serica solita Dawson, 1922. 1 ♂ paratype. 2431.
Serica ventura Dawson, 1932. 1 ♂, 3 ♀ paratypes. 2436.
Spilosota hirta pilosicollis Saylor, 1936. 1 paratype. 2459.
Strigodermella knausi Brown, 1925. 8 paratypes. 1154.
Trox (Trox) hamata Robinson, 1940. 4 paratypes. 3121.
Trox (Trox) plicatus Robinson, 1940. 1 paratype. 3119.
Trox robinsoni Vaurie, 1955. 6 ♂, 7 ♀ paratypes. 5395.
Trox (Trox) spinulosus Robinson, 1940. 1 ♂, 2 ♀ paratypes. 3120.
Trox (Omorgus) tytus Robinson, 1941. 7 ♂, ♀ paratypes. 5394.

Scolytidae

Cactopinus cactophthorus Wood, 1957. Great Basin Nat., 17: 105-106. ♂ holotype, ♀ allotype, 8 paratypes. 3124.
Cactopinus spinatus Wood, 1957. Great Basin Nat., 17: 106-109. ♂ holotype, ♀ allotype, 24 paratypes. 3126.
Chaetophloeus lasius Wood, 1956. Canadian Ent., 88: 251-252. ♀ holotype, ♂ allotype, 4 paratypes. 5631.
Chramesus crenatus Wood, 1956. Canadian Ent., 88: 257-258. ♂ holotype, ♀ allotype, 5 paratypes. 5638.
Chramesus quadridens Wood, 1956. Canadian Ent., 88: 256. ♂ holotype, ♀ allotype, 1 paratype. 5636.
Chramesus striatus Wood, 1956. Canadian Ent., 88: 256-257. ♂ holotype, ♀ allotype, 2 paratypes. 5637.
Chramesus xylophagus Wood, 1956. Canadian Ent., 88: 255-256. ♂ holotype, ♀ allotype, 1 paratype. 5635.
Cryphalus thatcheri Wood, 1954. Univ. Kans. Sci. Bull., 36: 994-996. ♀ holotype, ♂ allotype, 1 paratype. 5160.
Cryptocarenus porosus Wood, 1954. Univ. Kans. Sci. Bull., 36: 1014-1015. ♀ holotype, ♂ allotype. 5161.
Cryptocleptes subpilosus Wood, 1956. Canadian Ent., 88: 238. ♀ holotype, ♂ allotype. 5621.
Cyptocleptes minulus Wood, 1956. Canadian Ent., 88: 238-239. ♀ holotype, ♂ allotype, 2 paratypes. 5622.
Cryptocleptes yuccae Wood, 1956. Canadian Ent., 88: 239. ♀ holotype, ♂ allotype. 5623.

Dendroterus confinis Wood, 1959. Great Basin Nat., 19: 6-7. ♂ holotype, ♀ allotype, 4 paratypes. 3129.

Dendroterus decipiens Wood, 1959. Great Basin Nat., 19: 5-6. ♂ holotype, ♀ allotype, 2 paratypes. 3130.

Dendroterus mundus Wood, 1959. Great Basin Nat., 19: 3-4. ♂ holotype, ♀ allotype, 5 paratypes. 3147.

Hylocurus effeminatus Wood, 1956. Canadian Ent., 88: 143. ♂ holotype, ♀ allotype, 1 paratype. 5606.

Hylocurus equidens Wood, 1956. Canadian Ent., 88: 144, 146. ♂ holotype, ♀ allotype, 3 paratypes. 5604.

Hylocurus inaequalis Wood, 1956. Canadian Ent., 88: 146-147. ♂ holotype, ♀ allotype, 3 paratypes. 5603.

Hylocurus medius Wood, 1956. Canadian Ent., 88: 144. ♂ holotype, ♀ allotype, 3 paratypes. 5605.

Hylocurus nodulus Wood, 1956. Canadian Ent., 88: 141-142. ♂ holotype, ♀ allotype, 2 paratypes. 5607.

Hylocurus ruber Wood, 1956. Canadian Ent., 88: 142-143. ♂ holotype, ♀ allotype, 1 paratype. 5608.

Hypothenemus beameri Wood, 1954. Univ. Kans. Sci. Bull., 36: 1056-1058. ♀ holotype (right elytron broken), 25 paratypes. 5163.

Hypothenemus distinctus Wood, 1954. Univ. Kans. Sci. Bull., 36: 1065-1066. ♀ holotype. 5162.

Ips hunteri Swaine, 1917. Canad. Dept. Agr., Ent. Branch Bull. 14: 31. ♂ holotype, 6 paratypes. 1943.

Lathrotropis caseyi Blaisdell, 1906. Ent. News, 17: 71-73. 1 ♂ syntype. 1082.

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Scolytidae—Paratypes

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Silphidae s.l.—Paratypes

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Apsena rufipes simplex Blaisdell, 1932. 1 paratype. 1117.
Coelocnemis barretti Blaisdell, 1928. 3 paratypes. 2384.
Coniontis santarosae Blaisdell, 1921. 2 paratypes. 1122.
Eleodes acutangula Blaisdell, 1921. 1 paratype. 1120.
Eleodes (Litheleodes) vandykei modificata Blaisdell, 1921. 1 ♂ paratype. 1109.
Eleodes parowana Blaisdell, 1925. 3 paratypes. 1118.
Eleodes propinqua Blaisdell, 1918. 2 paratypes. 3418.
Eleodes tanneri Blaisdell, 1931. 1 paratype. 1119.
Platydema neglectum Triplehorn, 1965. 1 ♂, 1 ♀ paratypes. 6496.
Platydema wandae Triplehorn, 1965. 25 ♂, ♀ paratypes. 6497.

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A Review of the Genus Polygraphus[1]

DONALD F. J. HILTON

INTRODUCTION

There are three species of the genus *Polygraphus* in North America. Of these, *rufipennis*, known since 1837, has been described under three other names. This is not surprising when one realizes that the species is variable even within restricted areas of its range which extends over most of the coniferous forests of Canada and the United States, especially in regions where stands of white spruce, *Picea glauca*, occur.

There has been no synonymy in either *hoppingi* or *convexifrons*, the remaining North American species. Both have more restricted distributions and hosts than does *rufipennis*.

Polygraphus rufipennis is considered to be a secondary bark beetle since it usually attacks only dead or dying trees. However, Swaine (1918) states that at times it becomes a primary enemy of black and white spruce. He also states that, in a sense, it may be considered beneficial since it is among the species of scolytids which hasten the death of the lower branches of pine and spruce, thereby producing cleaner trunks which, in turn, produce better logs.

In Canada, *rufipennis* produces one to three generations a year, depending upon climatic conditions. Hibernation takes place, usually in the pupal or teneral adult stage, in the host's inner bark.

The majority of the field work for the biology of *Polygraphus rufipennis* was done during early spring and summer of 1966 five miles south of Seebe, Alberta. The experimental area has an elevation of 4560 feet and lies in the subalpine forest region. The main tree species are lodgepole pine (*Pinus contorta* var. *latifolia*), Engelmann spruce (*Picea engelmannii*), white spruce

[1] Contribution No. 1380 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

(Picea glauca), and the Engelmann-white spruce hybrid complex. Alpine fir *(Abies lasiocarpa)* occurs at higher elevations, whereas in the valley bottoms there are occasional stands of poplar *(Populus tremuloides* and *Populus balsamifera)*.

Climatic data of the experimental area for ten summers are given in Table 1.

TABLE 1. Climatic data for ten summers (1954-63) at Kananaskis Forest Experiment Station, Headquarters site. Precipitation is in inches, temperatures in degrees Fahrenheit.*

	May	June	July	Aug.	Sept.
Mean monthly precipitation	2.6	3.3	2.9	2.8	1.9
Mean monthly snowfall	10	....	....	....	4
Mean no. of days with precipitation	11	12	10	11	8
Monthly mean of daily max. temperatures	57	66	72	69	61
Monthly mean of daily min. temperatures	32	40	44	41	36
Extreme maximum temperature	82	87	90	89	86
Extreme minimum temperature	—7	27	30	29	19

* After MacHattie (1966).

ACKNOWLEDGMENTS

I wish to thank Dr. George W. Byers under whose direction this study was made, for his many ideas and helpful suggestions. To Dr. G. P. Thomas, I extend my sincere appreciation for allowing me to use the facilities of the Calgary Laboratory of the Canada Department of Forestry and Rural Development for this study. Mrs. Shirley Middleton, also of the Calgary Laboratory, reared beetles for me, and H. S. Whitney, a research officer at the Calgary Laboratory, identified the fungi. For their help I am very grateful.

I would also like to thank the following persons who loaned specimens in their care: especially Dr. S. L. Wood, Brigham Young University, Provo, Utah, who also provided many suggestions on the systematics of *Polygraphus*; D. E. Bright, Canada Department of Agriculture, Ottawa; O. L. Cartwright, United States National Museum, Washington, D.C.; P. J. Darlington, Jr., Museum of Comparative Zoology, Cambridge, Massachusetts; H. B. Leech, California Academy of Sciences, San Francisco; R. D, Lloyd, United States Department of Agriculture, Fort Collins, Colorado; J. A. Powell, University of California, Berkeley.

The following research staff members of the Canada Department of Agriculture, Entomology Research Institute, Ottawa, kindly made identifications of the insects and mites associated with *Polygraphus rufipennis*: D. E. Bright, W. J. Brown, J. M. Campbell, H. Howden, G. Lewis, E. E. Lindquist, W. R. M. Mason, O. Peck, G. S. Walley, and D. M. Wood.

The nematodes were identified by W. R. Nickle of the United States Department of Agriculture, Beltsville, Maryland.

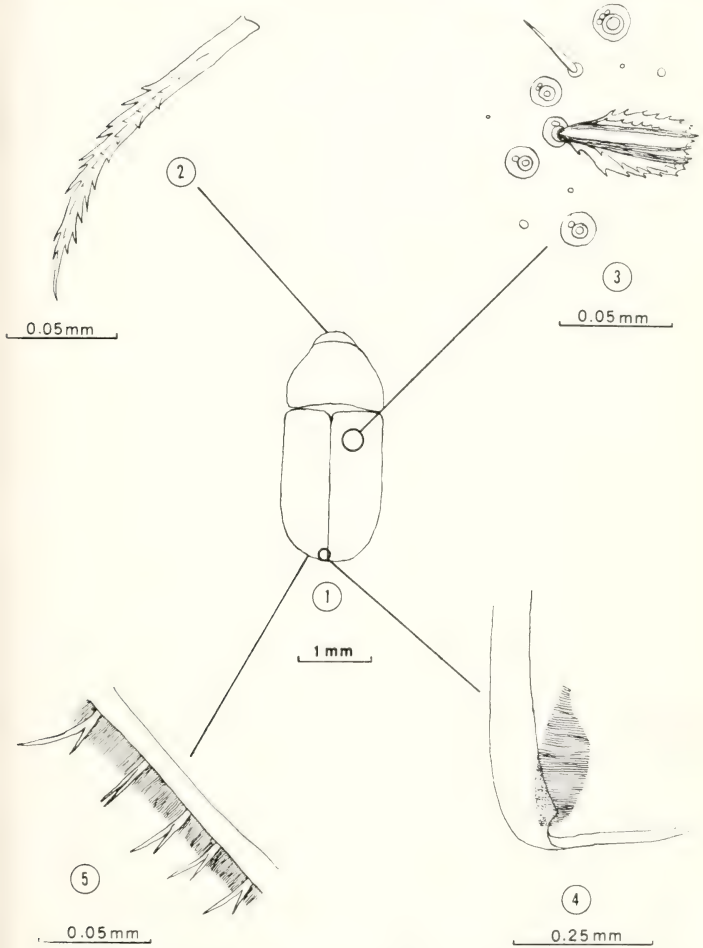
In conclusion I would like to express deep gratitude to my wife, Nora, for her help and encouragement during the course of this study.

MATERIALS AND METHODS

Laboratory reared *Polygraphus rufipennis* were kept in half-gallon or one-gallon cardboard tubs, to each of which was added a six-inch white spruce bolt for breeding material. The bolts had each end waxed to retard desiccation. Lids on the tubs prevented escape of the beetles.

All measurements were made with an ocular micrometer. Except for those on the head, measurements were taken from the dorsal aspect of each

beetle (Fig. 1). Body length is measured from the anterior edge of the exposed portion of the head to caudal tip of the elytra. Body width is measured at the bases of the elytra. Pronotal width is measured at its widest point



Figures 1-5. *Polygraphus* spp. 1, general body shape, 17×; 2, echinose seta from frons; 3, elytral scale and seta; 4, male stridulatory region; 5, bifurcate setae and brush border at edge of elytron.

(near the bases of the elytra), and its length is measured from anterior to posterior margin, along its midline. Width of the elytra is measured across the bases of both together, and elytral length is the distance from the base to the caudal tip measured along the elytral "suture." Head measurements are taken in frontal view (Figs. 15, 17); height is the distance from the center of the epistoma to the most anterior edge of the pronotum on the midline, and width is measured at the level of the dorsal margins of the eyes.

Microscopic characters such as body hairs (Figs. 2, 5, 12, 13), genitalia (Figs. 24-26), and tibial teeth (Figs. 9-11, 14) are often used as an aid to generic and specific diagnosis. For these characters to be examined in detail, the beetles must be dissected and their parts mounted on slides.

In the key to the species of *Polygraphus,* a character called the marginal tooth formula has been employed. This refers to the number of marginal teeth on each tibia. Thus a formula of 5-7-13 would mean that the protibia has five teeth, the mesotibia seven, and the metatibia 13. It should also be noted that a marginal tooth, rather than being merely a cuticular projection, has a socket (Fig. 14).

Drawings of undissected specimens were made with the aid of a camera lucida. A compound microscope drawing tube was used in illustrating slide mounted structures.

Measurements of 245 specimens were made as follows: *Polygraphus rufipennis* (Kirby), males 100, females 100; *Polygraphus hoppingi* Swaine, males 13, females 10; *Polygraphus convexifrons* Wood, males 19, females 3.

POLYGRAPHUS Erichson

Polygraphus Erichson, 1836. Archiv fur Naturgesch. Jahrg. 2, Vol. 1, p. 57.

The genus *Polygraphus,* as first proposed by Erichson, contained only one species, *Polygraphus pubescens.* This European species is synonymous with *Hylesinus pubescens* Fabricius, the type species, and *Dermestes poligraphus* Linnaeus. At present, there are 64 species recognized in the world fauna, three of which are found in America north of Mexico. Of the three American species, Kirby (1837) described *rufipennis* and placed it in the genus *Apate* (=*Lepisomus*). Within this genus, he also described *brevicornis* and *nigriceps,* which are now recognized as synonyms of *rufipennis.* R. N. Chrystal examined the types of both *brevicornis* and *nigriceps* and found that the latter differed from *rufipennis* only in having the head black with the pronotum and elytra light red. The type of *P. brevicornis* was so badly shattered as to be unrecognizable (Swaine, 1918). In 1853, Mannerheim described the species *saginatus* within the genus *Polygraphus* (Swaine, 1908). However, it again proved to be a synonym of *rufipennis.* Thus, *rufipennis* remained the only North American species until 1925, when Swaine described

hoppingi from Arizona. The third species, *convexifrons*, was described by Wood in 1951.

One fossil species is recognized in the genus, *Polygraphus wortheni*, described by Scudder in 1893 from the Roan Mountain Eocene of western Colorado.

DIAGNOSIS

Since the species of *Polygraphus* in general aspect resemble typical Hylesininae, only those morphological features not held in common with other members of the subfamily will be described. For a detailed, morphological treatment of a representative of the Hylesininae, the reader is referred to Richmond's 1935 study of *Dendroctonus monticolae* Hopkins.

Polygraphus is readily separated from all other genera in the subfamily by the possession of an unsegmented antennal club and by the fact that the eyes are almost completely divided, giving the beetles a four-eyed appearance. The adult beetles are piceous in color and range in length from 2.55 mm to 2.84 mm, and in width from 0.99 mm to 1.16 mm.

Head. (Figs. 15-22) Frons and anterior portion of vertex coarsely punctured; vertex, occipital, and genal regions finely but densely punctured. Frons in lateral view convex, flat, or concave, depending upon sex and species. Vestiture on frons varying from dense long yellow hairs in female *hoppingi* to scattering of fine short hairs in female *convexifrons*; long golden hairs from epistoma and hypostoma covering basal one-fourth or more of mandibles; long hairs (setae) on frons echinose (Fig. 2), short hairs simple. Males have two median tubercles, sometimes merged to form one, on frons between eyes; these absent in females. Antenna (Figs. 6-8) composed of scape, 5 to 6 segmented funicle (basal segment of which is pedicel) and flattened, unsegmented club. Scape as long as club, slightly more than twice as long as funicle, narrow at base, widened distally, clavate. Pedicel largest segment of funicle, narrow basally, widened distally, its greatest width equaling its length, its distal end strongly rounded. Second segment of funicle also narrow at base and widened distally until width is equal or subequal to length; in contrast to that of pedicel, its distal end truncate. Remaining 4 to 5 segments of funicle equal or subequal, 2.5-3.0 times as wide as long. Club 2.5 times as long as its greatest width, round at base, tapering to slightly or strongly acuminate apex, with dense vestiture composed of simple setae and setae echinose on one side only (Fig. 12). Scape and funicle with only a few scattered setae, echinose, echinose on one side only, or simple.

Pronotum. Wider than long (see species descriptions), narrowed anteriorly (Fig. 1), with a faint longitudinal median carina running length of pronotum; anterior margin moderately rounded; dorsal surface coarsely punctate, covered with scales similar to those on elytra (Fig. 3); sides less

coarsely punctate, without scales; brushes of fine hairs directed cephalad along anterior margin of pronotum and directed caudad along postero-ventral margins.

Elytra. Longer than wide (see species descriptions); lateral margins parallel; anterior margin transverse to faintly arcuate; posterior margin strongly curved; humeri narrowly rounded; declivity convex; bases of elytra feebly denticulate, rest of elytral surface punctulate, scarcely striate, densely clothed with small stout scales and with rows of subequal, simple setae (Fig. 3); posterior and lateral edges of elytra with a border of fine hairs; bifurcate setae interspersed with this brush border at regular intervals (Fig. 5). In males, an oval, transversely striated region on underside of posterior end of each elytron on either side of the elytral suture (Fig. 4). (These regions are used as a stridulatory organ when the male rubs the last two abdominal terga against them by moving the end of the abdomen up and down.)

Ventral body surface. Completely covered by fine golden pubescence similar to that found on leg segments (Fig. 13).

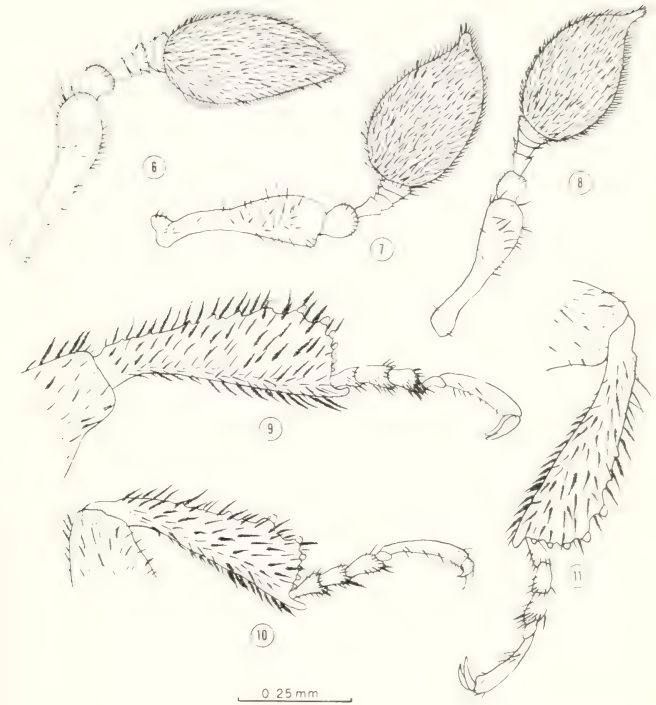
Legs. Fore coxae globose and contiguous; mesocoxae subglobose, separated by one-half their width; metacoxae transverse, separated by slightly less than distance separating mesocoxae. Third tarsal segment not bilobed. Number of marginal teeth on tibiae variable, depending upon species and sex (Figs. 9-11) (see species descriptions). All leg segments covered by fine golden pubescence of setae which are simple, echinose, or echinose on one side only (Fig. 13).

MALE *genitalia* (Figs. 23-26) composed of spiculum gastrale, two median lobes united dorsally, two median struts, tegmen, and transfer apparatus. Spiculum gastrale ventrale, strongly arcuate, slightly longer than combined length of median lobes and median struts, with a short projection or spur one-third of its length from posterior end. Immediately dorsal to spiculum gastrale lie halves of median lobe; each half narrowing abruptly anteriorly to form two median struts. Median struts bent acutely at bases, angled dorsally, equal or subequal in length to median lobes. Transfer apparatus surrounded by median lobes, lightly sclerotized, very difficult to see, approximately 0.75 times as long as median structs. Tegmen surrounding dorsal side of median lobes at point where median struts begin, C-shaped with closed end dorsal and inclined anteriorly, free ends directed postero-ventrally. Tegmen without tegmenal strut seen in genus *Ips*, but in *hoppingi* and *convexifrons* a tiny projection present where tegmenal strut would be.

FIGURES 6-8. Antennae of males. 6, *Polygraphus rufipennis*; 7, *Polygraphus hoppingi*; 8, *Polygraphus convexifrons*.

FIGURES 9-11. Mesotibiae and tarsi of males. 9, *Polygraphus rufipennis*; 10, *Polygraphus hoppingi*; 11, *Polygraphus convexifrons*.

FIGURES 12-14. Structural details of *Polygraphus* spp. 12, setae on antennal club; 13, setae on tibia, 14, marginal tooth and tibial projections.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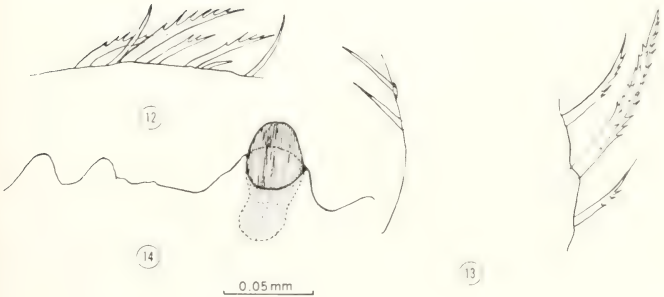
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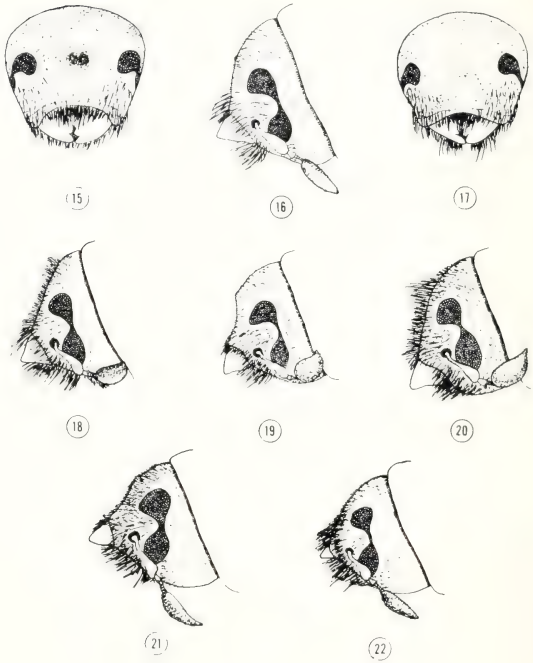
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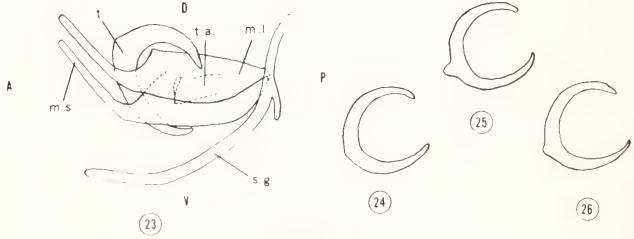
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KEY TO THE SPECIES OF POLYGRAPHUS

1. Hair on frons very short and sparse. Frons either flat or concave, with one or two median tubercles dorsal to concavity (males) 4
   Hair on frons long, dense, and golden. Frons essentially flat with no tubercles (except *convexifrons*, where it is convex and has no long pubescence) (female) 2
2. Apex of antennal club not acuminate, or only moderately so; marginal tooth formula 4-6-8 or 4-5-7; frons flat, with long, golden pubescence 3
   Apex of antennal club strongly acuminate; marginal tooth formula 4-6-8; frons convex; without long, golden pubescence ..... *convexifrons*
3. Apex of antennal club moderately acuminate; hypostomal pubescence short, not extending below tip of mandibles in frontal view; marginal tooth formula 4-6-8 ..... *hoppingi*
   Apex of antennal club not acuminate; hypostomal pubescence long, extending below tip of mandibles in frontal view; marginal tooth formula 4-5-7 ..... *rufipennis*
4. Frons below median tubercles concave; apex of antennal club strongly or moderately acuminate; marginal tooth formula other than 5-7-13 5
   Frons below median tubercles flat; apex of antennal club not acuminate; marginal tooth formula 5-7-13 ..... *rufipennis*
5. Short pubescence extending into emargination of eye; apex of antennal club strongly acuminate; marginal tooth formula 4-5-7 ..... *convexifrons*
   Short pubescence not extending into emargination of eye; apex of antennal club moderately acuminate; marginal tooth formula 4-6-8 ..... *hoppingi*

Polygraphus rufipennis (Kirby)

Apate (=Lepisomus) rufipennis Kirby, 1837. Faun. Bor. Am. 4:193.
Apate (=Lepisomus) brevicornis Kirby, 1837. Faun. Bor. Am. 4:194.
Apate (=Lepisomus) nigriceps Kirby, 1837. Faun. Bor. Am. 4:194.
Polygraphus saginatus Mannerheim, 1853. Bull. Moscou 26:237.

Schedl (1957) regarded *rufipennis* as a synonym of the European *poligraphus*, but Wood (1966) examined both species very closely and feels that they are distinct since there are more consistent differences between them than there are between many other species in the genus.

Female. Body length 2.59 mm; width 1.12 mm.

Head (Figs. 17, 18) 1.36 times as wide as high. Frons in lateral view relatively flat. Dense vestiture of golden hair extending from vertex to epistoma, long at vertex and epistoma and short on frons so that outline of vestiture in lateral view is concave. Dense growth of hair arising from

Figures 15-18. *Polygraphus rufipennis* heads. 15, male, front view; 16, male, lateral view; 17, female, front view; 18, female, lateral view.

Figures 19-22. *Polygraphus* spp., heads in lateral view. *Polygraphus hoppingi*: 19, male; 20, female. *Polygraphus convexifrons:* 21, male; 22, female.

Figure 23. Male genitalia of *Polygraphus rufipennis*, ventro-lateral view. A, anterior; D, dorsal; P, posterior; V, ventral; s.g., spiculum gastrale; m.l., median lobe; m.s., median strut; t, tegmen; t.a., transfer apparatus.

Figures 24-26. Tegmina of *Polygraphus* spp., ventral view. 24. *Polygraphus rufipennis*: 25, *Polygraphus hoppingi*; 26, *Polygraphus convexifrons.*

hypostoma, in frontal view extending below lower margin of mandibles. Antennal funicle usually 6 segmented, occasionally 5; antennal club with tip not acuminate, or only very slightly so (Fig. 6).

Tibiae. Four marginal teeth on protibia, 5 on mesotibia, and 7 on metatibia.

Pronotum 1.43 times as wide as long.

Elytra 1.58 times as long as wide.

MALE. Body length 2.55 mm; width 1.14 mm.

Head (Figs. 15, 16) 1.25 times as wide as high. Frons in lateral view relatively flat. Vestiture on frons and vertex short, very sparse except for epistomal and hypostomal regions, where hair is dense, covering base of mouthparts, although (in frontal view) not extending as far below tip of mandibles as in female. Antennae as in female (Fig. 6).

Tibiae. (Fig. 9) Five marginal teeth on protibia; 7 on mesotibia, and 13 on metatibia.

Pronotum 1.53 times as wide as long.

Elytra 1.52 times as long as wide.

Genitalia. (Figs. 23-24) Antero-dorsal margin of tegmen smoothly and strongly arcuate; tegmenal projection absent.

TYPES. Two males were taken at Latitude 65° in N.W.T. Canada, probably near Fort Franklin on the S.W. shore of Great Bear Lake, by Sir John Richardson and deposited in the British Museum (Natural History), London.

HOSTS (Fig. 27). Of the following hosts recorded for *rufipennis* it can be seen from Fig. 27 that the spruces, and in particular *Picea glauca*, are the most favored by this beetle.

Abies balsamea, A. concolor, A. fraseri, A. lasiocarpa, Larix sp., *L. laricina, L. occidentalis, Picea* sp., *P. canadensis, P. engelmannii, P. glauca, P. mariana, P. pungens, P. rubens, Pinus banksiana, P. contorta, P. monticola, P. ponderosa, P. resinosa, P. strobus, P. sylvestris, Pseudotsuga taxifolia, Tsuga heterophylla*.

DISTRIBUTION. A separate map (Fig. 28) has been made to show the distribution of *rufipennis* in Alberta, Canada, where the major part of the biological study was done. The Canada Department of Forestry and Rural Development gave me access to its collection records at the Calgary Laboratory, and I felt that the localities would be best plotted on a map since there were 134 collections recorded by grid number rather than by nearest town or post office.

Specimens have been examined from the following localities in the rest of Canada and the United States.

CANADA. BRITISH COLUMBIA: Barkerville; Bowser; Campbell River; Lorna; Lumby; Merritt; Mogle Mountain; Moyie Mountain; Princeton; St. Steek; Stanley; Terrace; Trinity

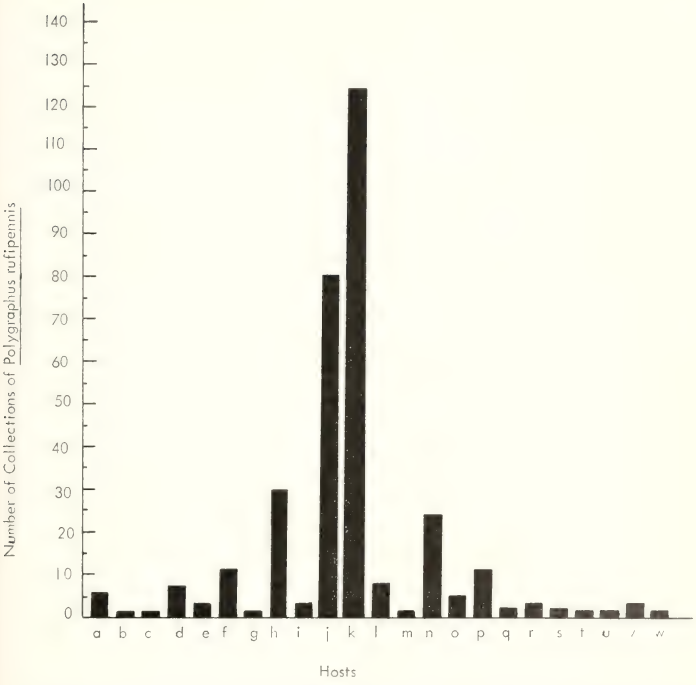


Figure 27. Histogram showing distribution of collections of *Polygraphus rufipennis* from the following hosts: a, *Abies balsamea;* b, *A. concolor;* c, *A. fraseri;* d, *A. lasiocarpa;* e, *Larix* sp.; f, *L. laricina;* g, *L. occidentalis;* h, *Picea* sp.; i, *P. canadensis;* j, *P. engelmannii;* k, *P. glauca;* l, *P. mariana;* m, *P. pungens;* n, *P. rubens;* o, *Pinus banksiana;* p, *P. contorta;* q, *P. monticola;* r, *P. ponderosa;* s, *P. resinosa;* t, *P. strobus;* u, *P. sylvestris;* v, *Pseudotsuga taxifolia;* w, *Tsuga heterophylla.*

Valley. Labrador: Goose Bay. Manitoba: Aweme; Onah; Red Deer River; Riding Mountain; Winnipeg. New Brunswick: Bantalor, York Co.; Bathurst; Blissfield, Northumberland Co.; Fredericton; Lower Gagetown, Queens Co.; Maple Grove; McGivney, York Co.; Narrows, Queens Co.; Penobsquis; Pisiquil River; Prosser Brook, Albert Co.; St. Margarets; Turtle Creek, Albert Co.; Waterford, Kings Co. Newfoundland: Grand Falls; Little River. Northwest Territories: Aklavik; Fort Smith; Great Slave Lake; Reindeer Depot, Mackenzie Delta. Nova Scotia: Kemptville East, Yarmouth Co.; Medway; Truno; Westchester Lake; Weymouth. Ontario: Algonquin Park; Ottawa; Paris; Scotia Junction; Timagami; Wooler. Prince Edward Island: Eldon, Queens Co.; Miscouche, Prince Co.; Montague, Kings Co. Quebec: Bouch-ile; Gaspe Co.; Lake Memphre-magog; Lauiel; Montreal; Mt. Lyell; Queen's Park, Aylmer; St. Anne's; Stoke; Thunder River. Saskatchewan: Cypress Hills.

UNITED STATES. Alaska: Anchorage; Juneau; Kasilof; Matanuska; Mt. McKinley National Park; Nakaek Lake. Colorado: Jackson Co.: New Castle, White River National Forest; Rabbit Ears Pass, Routt National Forest; Rand; Rio Grande National Forest; Stove Prairie, Roosevelt National Forest; Uncompahgre National Forest. Idaho: Coeur d'Alene; Enaville; Krassel Ranger Station, Valley Co.: Magee; Magruder Ranger Station, Idaho Co.: Martin Creek.

Valley Co. Indiana: Lafayette; Stoke. Maine: Kineo, Lincoln Co.; Medomak; Monmouth; Mt. Katahdin; Orono; Southport; Wales. Massachusetts: Ashland; Law; Melrose; Mt. Tom; Petersham; Stoneham; Sunderland. Michigan: Deward; East Lansing; Mackinac; Marquette; Ottawa National Forest. Minnesota: Almstead Co.; Cloquet; Duluth; Ely; Hennepin Co.; Hubbard Co.; Itasca Park; Ithaca Park; Lake Co.; Lake Itasca; Mille Lacs Co. Montana: Bozeman; Glacier National Park; Nine Mile Creek, Missoula Co.; Pray; Ross Creek; Yellowstone National Park. New Hampshire: Bartlett; Great Gulf Trail, Mt. Washington; Lakes of the Clouds, Mt. Washington; Pittsburg; Waterville; White Mountains. New Mexico: Beulah; Santa Fe Ski Basin, Santa Fe Co. New York: Catskill Mountains; Chateaugay Lake; Cranberry Lake; Fourth Lake, Fulton Chain; Lewis Co.; Mt. Seward; Syracuse; Upper Saranac Lake. North Carolina: Black Mountains; Cherokee; Mt. Mitchell. Oregon: Corvallis; Ft. Klamath; Klamath Falls; Mohler, Clatsop Co.; Odell Lake; Santiam Junction, Linn Co.; Santiam Pass; Suttle Lake; Tollgate; Willamette Pass, Lane Co. Pennsylvania: Jeannette, Westmoreland Co.; North Mountain, Sullivan Co.; Pocono Lake; Tamarack. South Dakota: Lead; Weta. Tennessee: Gatlinburg; Great Smokey Mountain National Park. Utah: Beaver; Grandaddy Lakes, Uintah Mountains; La Sal Mountains, San Juan Co.; Logan Canyon; Mirror Lake, Summit Co.; Paradise Park; Puffer Lake, Beaver Co.; Wolf Creek Pass. Vermont: Jay Peak; Mt. Mansfield; Wilmington. Washington: Evans Creek, King Co.; Kooskooskie; Metaline Falls; Mt. Rainier National Park; Nahcotta; Parkway; Plain; Winthrop. Wisconsin: Bayfield Co.; Clintonville. Wyoming: Gypsum Creek, Moose Creek, Bridger National Forest; Little Medicine; Saratoga; Yellowstone National Park.

Polygraphus hoppingi Swaine

Polygraphus hoppingi Swaine, 1925. Can. Ent. 57:51.

Female. Body length 2.55 mm; width 1.02 mm.

Head (Fig. 20) 1.4 times as wide as high. Frons in lateral view relatively flat. Dense vestiture of golden hair extending from vertex to epistoma, forming concave profile as in female *rufipennis* but 1.3-1.5 times as long as in that species; hair on epistoma and hypostoma shorter and less dense than in female *rufipennis* and in frontal view not extending below lower margin of mandibles. Antennal funicle 5 segmented; apex of antennal club moderately acuminate (Fig. 7).

Tibiae. (Fig. 10) Four marginal teeth on protibia, 6 on mesotibia, and 8 on metatibia.

Pronotum 1.38 times as wide as long.

Elytra 1.72 tmes as long as wide.

Male. Body length 2.62 mm; width 1.07 mm.

Head (Fig. 19) 1.4 times as wide as high. Frons in lateral view concave below frontal tubercles. Vestiture on head very short, sparse, except long enough on hypostoma and epistoma to cover bases of mouthparts; in frontal view hypostomal pubescence not extending below lower margin of mandibles. Antennae as in female (Fig. 7).

Tibiae. (Fig. 10) Number of marginal teeth same as on respective tibiae in female.

Pronotum 1.38 times as wide as long.

Elytra 1.67 times as long as wide.

Genitalia. (Fig. 25) Antero-dorsal margin of tegmen smoothly and strongly arcuate except for rounded median tegmenal projection, one-third length of spur on spiculum gastrale.

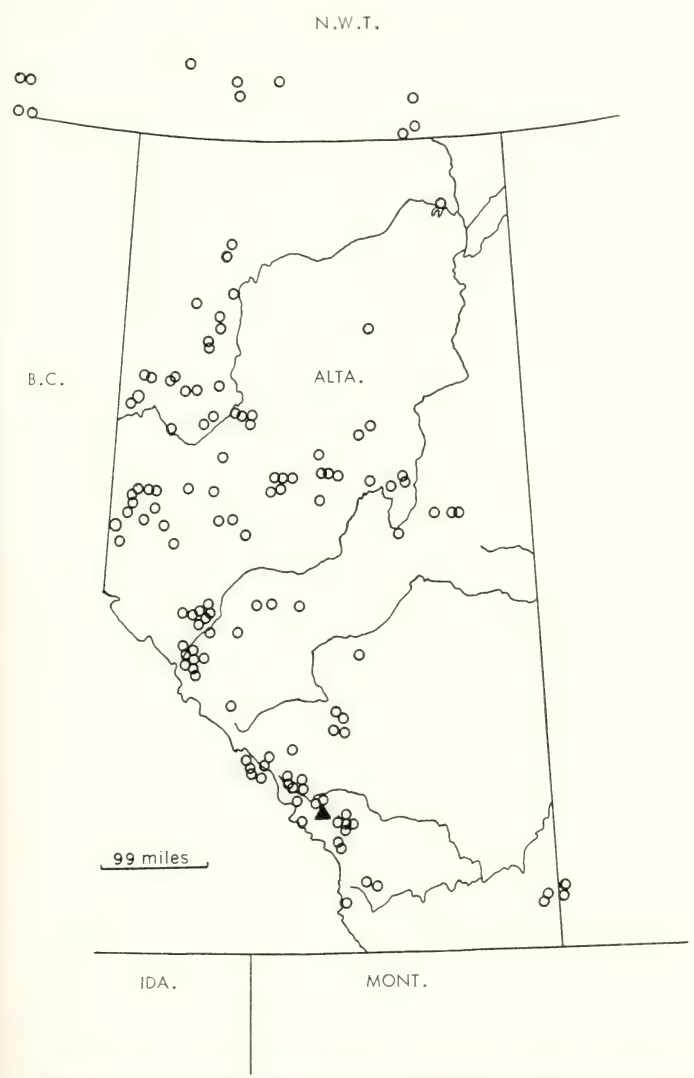


Figure 28. Map of Alberta showing distribution of *Polygraphus rufipennis*. Dark triangle indicates main field study area near Seebe.

TYPES. The female holotype and male allotype were collected from *Picea engelmannii* on San Francisco Peak, Arizona, June 20, 1918, by Ralph Hopping; type No. 1329 in the Canadian National Collection, Ottawa. The only paratype, a female, has the same label data but was deposited in the collection of *R. Hopping*, which has since become the property of the California Academy of Sciences.

HOSTS. The only host recorded for *hoppingi* is *Picea engelmannii*.

DISTRIBUTION. *Polygraphus hoppingi* apparently has a very restricted range. Specimens have been examined from the following localities:

UNITED STATES. ARIZONA: Grand Canyon National Park; San Francisco Peak. COLORADO: Mesa. NEW MEXICO: no specific locality.

Polygraphus convexifrons Wood

Polygraphus convexifrons Wood, 1951. J. Kans. Ent. Soc. 24:31-32.

FEMALE. Body length 2.59 mm; width 1.12 mm.

Head (Fig. 22) 1.36 times as wide as high. Frons in lateral view convex. Pubescence on head very short and sparse except long enough on epistoma and hypostoma to cover bases of mouthparts; in frontal view hypostomal pubescence extending either to, or slightly below, lower margin of mandibles. Antennal funicle 5 segmented; apex of club strongly acuminate (Fig. 8).

Tibia. Four marginal teeth on protibia, 6 on mesotibia, and 8 on metatibia.

Pronotum 1.35 times as wide as long.

Elytra 1.89 times as long as wide.

MALE. Body length 2.84 mm; width 1.16 mm.

Head (Fig. 21) 1.50 times as wide as high. In lateral view frons concave below frontal tubercles. Frontal tubercles more often absent in this species than in either of other two. Pubescence short on frons and vertex, extending into eye emargination; hypostomal and epistomal pubescence long, as in other species, extending over bases of mouthparts; in frontal view hypostomal vestiture not extending below lower margin of mandibles. Antennae as in female (Fig. 8).

Tibiae (Fig. 11). Four marginal teeth on protibia, 5 on mesotibia, and 7 on metatibia.

Pronotum 1.35 times as wide as long.

Elytra 1.68 times as long as wide.

Genitalia. (Fig. 26) Antero-dorsal margin of tegmen smoothly and strongly arcuate except for small rounded median tegmenal projection, one-fourth length of spur on spiculum gastrale.

TYPES The male holotype and four female paratypes were collected by S. L. Wood from *Picea engelmannii* in Logan Dry Canyon, Utah, on June 11, 1949. The female allotype and nine female paratypes have the same collector and host but were collected from Logan Canyon, Utah, on July 6,

1948. The holotype, allotype, and four paratypes are deposited in the United States National Museum, Washington, D. C., and the remaining paratypes are in the collection of S. L. Wood, now at Brigham Young University, Provo, Utah.

Hosts. *Picea canadensis* and *P. engelmannii* are the only hosts recorded for *convexifrons*.

Distribution. *Polygraphus convexifrons* has a somewhat greater distribution than *hoppingi*. Specimens have been seen from the following localities:

UNITED STATES: Alaska: Mt. McKinley National Park. Utah: Beaver: La Sal Mountains; Logan Canyon; Logan Dry Canyon. Wyoming: Saratoga.

BIOLOGY OF POLYGRAPHUS RUFIPENNIS

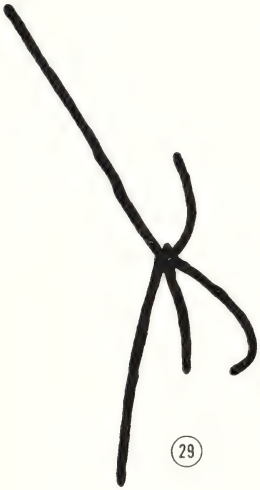
Spring emergence. Under field conditions adult beetles which have overwintered in the host trees emerge during the last two weeks in May and the first two in June. They then fly in search of new hosts, usually dead or dying spruces. If the beetles have overwintered in either the larval or pupal stage, the date of emergence will be two to six weeks later.

Entrance hole. As the beetles find new hosts, the female is the first to bore into the bark. The entrance hole, made at an angle of about 45° to the surface, is usually hidden under a scale of bark, although its position can be determined by the fine boring dust scattered nearby.

Nuptial chamber. Once inside the inner bark, the female cuts out the nuptial chamber, a task which takes two to three days. Upon completion, or near completion, she is joined by a male and mating takes place. The female mates only once while in this particular gallery because the male is prevented from reaching her again by the boring dust which she pushes behind her as she progresses in her egg tunnel. It is possible, however, that the female mates again after she leaves her first gallery in midsummer and begins a new one in another tree, or in a different portion of the same tree.

During construction of both the nuptial chamber and egg tunnel she lightly scores the sapwood.

The male remains in the nuptial chamber and, keeping it free of boring dust, very gradually enlarges it. He also makes short feeding tunnels from various sides of the chamber (Fig. 31). After the first female has begun her egg tunnel, from one to three additional females enter the nuptial chamber, mate, and begin egg tunnels. The second female to arrive usually constructs her tunnel on the side of the nuptial chamber opposite that of the first female (Figs. 31, 32). Each female thereafter positions her egg tunnel as far as possible from the others so that when four or five females are present the galleries radiate (Fig. 29). The usual number of females per gallery is two, but there may be one, or as many as five so that the galleries range from uniramous to pentaramous (Figs. 29-33).



30 mm

FIGURES 29-33. Egg tunnels and nuptial chambers of *Polygraphus rufipennis*. 29, pentaramous; 30, triramous; 31, biramous showing short feeding tunnels of male; 32, biramous; 33, triramous with the third egg tunnel only recently begun.

At about the same time as the females leave the egg tunnels (see following section on egg tunnels), the male abandons the nuptial chamber and seeks a new one just started by a female.

Egg tunnels. If there are only one or two females in the gallery, the egg tunnels are usually constructed at right angles to the grain of the wood. When three or more females are present, some of the tunnels run with the grain.

For about four weeks the female, laying eggs as she goes, continues to lengthen her tunnel to 70-100 mm. She then bores an exit hole at the end of the tunnel and, if it is July or early August, leaves to begin another egg tunnel on a new tree, or in a different part of the same tree. If it is late August when the female completes her egg tunnel, she will remain within it over the winter. If it is her first breeding season, she will probably live through the winter and construct another gallery next spring, while an old (i.e., second year) female usually dies during hibernation.

Egg niches. After the female has constructed approximately 10 mm of the egg tunnel, she begins to cut semicircular egg niches into either side of it. No particular pattern is followed in their placement. Sometimes niches will be excavated opposite one another; other times several will be constructed side by side before any are cut into the opposite side of the tunnel. On the average, there are 20 egg niches per egg tunnel.

Upon completion of each egg niche, the female deposits one egg in it, then packs the niche with boring dust until the dust is flush with the sides of the egg tunnel. The egg is thus concealed and protected from predators.

Occasionally no egg will be deposted in a niche, but the female proceeds to pack it with boring dust just as though there were an egg present.

Eggs. The eggs, which are pearly white and oval in outline with a smooth chorion, have a mean length of 0.78 mm and a mean width of 0.45 mm. Their incubation period is five to six days under the average temperature given in Table 1. However, the incubation period will be more prolonged under considerably cooler conditions.

Larvae. The larvae, typically scolytid in form, are C-shaped, whitish in color, with a brown, strongly sclerotized head capsule. There are three instars (Fig. 34). The head capsule of the first instar has a mean width of 0.37 mm, of the second a mean width of 0.48 mm, and of the third a mean width of 0.61 mm.

Upon eclosion, the larvae burrow away at right angles from the egg tunnel, essentially maintaining this direction unless they run into an obstacle such as an egg tunnel, another larval mine, or the base of a branch.

The three larval stages combined last an average of 25 days. During this time, the larvae are continually feeding (except for a short quiescent period of 2-5 days just prior to pupation) and thus lengthening their tunnels until,

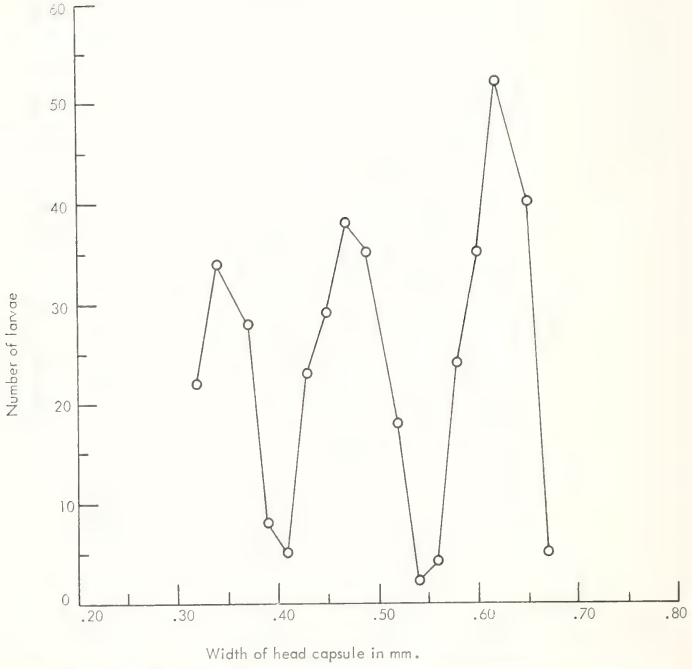


FIGURE 34. Graph indicating number of larval instars of *Polygraphus rufipennis*.

at the time of pupation, the mines are 50-100 mm long. As the larvae progress in their tunnels, they push the frass and boring dust behind them so that the mines become plugged.

During the first and second instars, the larvae burrow in the inner bark and do not score the sapwood. However, the third instar is large enough to score the sapwood during the last few days of its development, especially when it excavates the pupal chamber.

Pupae. At the end of its development, the larva excavates an oval pupal chamber and pupates. The pupa is typically scolytid and at first glistening white. During its seven to ten-day pupal stage, it gradually darkens to a light tan. Its mean length is 2.73 mm and the mean width 1.05 mm.

Adults. After emergence from the pupal skin, the teneral adult is a very light tan color. The newly emerged adults remain in the pupal chamber, and in the next few weeks their color gradually deepens to piceous. By slowly

feeding, they enlarge the cavity to a diameter of 8-10 mm. They then hibernate in this feeding chamber and emerge the following spring to begin breeding.

Sexing 596 laboratory-reared beetles revealed 35 % males and 65 % females.

Overwintering. The progeny from the first set of eggs, laid by the female in June, having reached the adult stage by July, overwinter as teneral adults. The progeny from the late July or early August batch of eggs hibernate as larvae, pupae, or teneral adults, depending upon the speed of development which, in turn, is dependent upon weather conditions.

Although hibernation is temperature-induced in the field, the beetles seem to have obligatory diapause. This was evident in beetles in ten sections of white spruce logs kept in the laboratory at room temperature from June, 1966, until May, 1967. They ceased activity around the middle of September, 1966, and have not resumed it as of May, 1967. On the other hand, four infested white spruce logs which were in the laboratory since June, 1966, were put into cold storage on September 1, 1966, at a constant temperature of 0° C. These logs were removed from the cold environment on December 1, 1966. The beetles began to emerge on December 15, 1966, and continued to do so for the next 55 days.

Total length of life cycle (Fig. 35). Adults which have overwintered begin to emerge during the last week of May or the first week of June and are designated as A1 adults for the purposes of Fig. 35. They then infest new breeding material and lay eggs. From these develop the brood that reaches the adult stage (A2) during the last week in July but remains in the bark feeding until the onset of winter induces hibernaton. They (A2) emerge in late May or early June of the next year to begin gallery construction.

While the A2 adults are emerging from the pupal stage, the A1 adults leave the first galleries and seek new breeding material (either the same or a different tree), to begin the second set of galleries. Some of the A3 brood so produced begin to emerge from pupation during the first week of September, and as adults feed in the bark until hibernation. These emerge the next year at the same time as the A2 adults.

Unlike the first brood, the second brood may either undergo hibernation as larvae or pupae. A3 adults from overwintered larvae and pupae emerge the next year during the last two weeks of June and the first week of July respectively.

The A1 adults remain in the second set of galleries, feeding until hibernation takes place. Some perish during the winter months, but those that survive construct one or two sets of galleries the following year.

Thus, in southwestern Alberta there are nearly always two broods per season because A1 adults have two broods in the first season and one or two

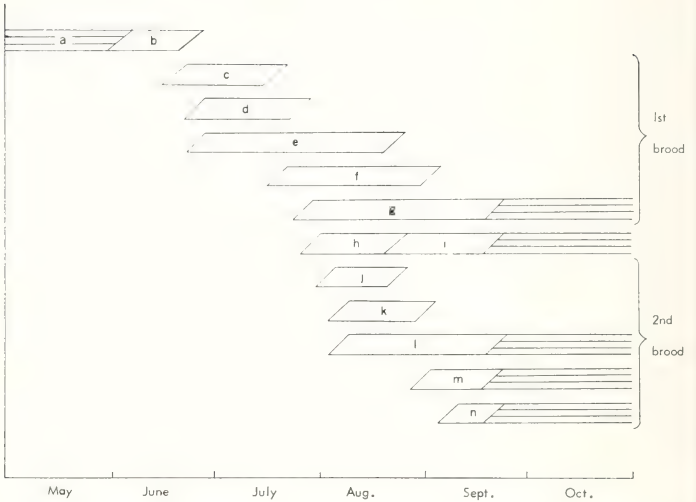


FIGURE 35. Generalized life cycle of *Polygraphus rufipennis* in southwestern Alberta. a, overwintering; b, A1 adults emerge; c, eggs laid; d, eggs hatch; e, larvae; f, pupae; g, A2 adults; h, A1 adults leave first galleries and start new ones; i, A1 adults feed; j, eggs laid; k, eggs hatch; l, larvae; m, pupae; n, A3 adults.

in the second season, while A3 adults (from overwintering larvae and pupae) have only one brood in the first season, two in the second, and perhaps one in the third season (if they live through the second winter as adults).

The number of broods per season depends upon the locality. There may be only one in northern areas such as the Yukon, or as many as three in more southern localities.

Associated bark or wood-inhabiting beetles. Twelve, four foot sections of field-infested white spruce logs were held in cages in the laboratory and all emerging insects were collected, including the following species of beetles: Buprestidae, *Melanophila drummondi* Kirby; Cerambycidae, *Neoclytus muricatulus* (Kirby), *Pogonocherus penicillatus* LeConte; Colydiidae, *Lasconotus intricatus* Kraus; Cucujidae, *Leptophloeus alternans* (Erickson); Curculionidae, *Magdalis alutacea* LeConte, *Rhyncolus brunneus* Mannerheim; Lathridiidae, *Corticaria* sp.; Scolytidae, *Carphoborus intermedius* Wood, *Dryocoetes affaber* (Mannerheim), *Pityophthorus murrayanae* Blackman, *Scolytus piceae* Swaine, *Trypodendron lineatum* (Oliver); Staphylinidae, *Isomalus mancus* Casey; Tenebrionidae, *Corticeus* sp., *Tribolium confusum* Jacquelin du Val.

Price (1966), in a study comparing the suitability of black, red, and white spruce as hosts for *Polygraphus rufipennis*, found that the larval mines were longer (and there were more adults per square decimeter) in red spruce than in white spruce. In each case, black spruce was intermediate between red and white spruce. Price also found that in white spruce there were twice as many square decimeter bark samples affected by competing agents than in red spruce, with black spruce again being intermediate. The competing agents considered by Price were Coleoptera (Scolytidae-*Dryocoetes* spp., *Ips pini*; Cerambycidae-*Monochamus scutellatus*) and fungal growth. He felt that the reason white spruce is the least favorable of the three for development of *Polygraphus rufipennis* is due to the severe competition within the bark. Red spruce has scalier bark which is at least twice as thick as that of black and white spruce. For this reason, it may not be as favorable a host for the competing species.

Associated fungi. Adult *Polygraphus rufipennis* were field collected from infested white spruce logs. They were brought into the laboratory, caged with fresh, uninfested white spruce and left for two months. Agar cultures were then made from the insects and from their burrows and the following genera of fungi were identified:

Source of fungi	Fungi
boring dust	*Penicillium* sp.
egg tunnel	*Leptographium* sp.
	Penicillium sp.
	Trichoderma sp.
larval tunnel	*Penicillium* sp.
pupal chamber	*Trichoderma* sp.
larva	*Leptographium* sp.
	Sporotrichium sp.
	Trichoderma sp.
pupa	*Graphium* sp.
	Trichoderma sp.
adult	*Graphium* sp.
	Trichoderma sp.

There is no correlation between the life stages of the beetles or the location in the gallery and the genera of fungi found. These fungi are all saprophytic, are nonpathogenic to either the beetle or the tree, and are typically associated with many other species of scolytids.

Parasites and predators. In this study, I was unable to find any trees which were infested solely with *Polygraphus rufipennis*. Since most scolytid larvae look alike, I could not say that any of the parasites and predators I found came from, or attacked, only *P. rufipennis*. However, I have been

able to compile the following list of parasites and predators from the literature (Bushing, 1965; Chamberlin, 1939; Craighead, 1950; Reid, 1957). The genera or species marked with an asterisk are ones which I also reared from white spruce logs field infested with *Polygraphus rufipennis* and other scolytid species.

Parasites. Insecta: Hymenoptera; Braconidae—*Cosmophorus hopkinsii* Ashmead, *Heterospilus pityophthori* Ashmead, *Heterospilus* sp., *Spathius claripennis* Ashmead, **Spathius* sp., *Spathius tomici* Ashmead. Eurytomidae—*Decatomidea polygraphi* Ashmead, **Eurytoma* sp., *Ipideurytoma polygraphi* Ashmead. Pteromalidae—**Cecidostiba acuta* (Provancher), *Cecidostiba dendroctoni* Ashmead, *Cecidostiba polygraphi* Ashmead, *Cheiropachus* sp., *Heydenia unica* Cook & Davis, **Rhopalicus pulchripennis* (Crawford), *Rhopalicus* sp. Torymidae—*Liodontomerus* sp., *Roptrocerus eccoptogastri* Ratzburg, **Roptrocerus xylophagorum* Ratzburg.

Predators. Insecta: Coleoptera; Cleridae—*Thanasimus nigriventris* LeConte. Corynetidae—*Phyllobaenus dislocatus* Say. Histeridae—*Paromalus bistriatus* Erichson. Staphylinidae—*Quedius peregrinus* Gravenhorst, *Xantholinus cephalus* Say. Tenebrionidae—*Corticcus glaber* LeConte, *Corticeus thoracicus* Melsheimer. Diptera; Dolichopodidae—*Medeterus aldrichii* Wheeler, *Medeterus ciliata* Van Duzee, *Medeterus nigripes* Loew.

Aves: Piciformes; Picidae—*Dendrocopus villosus.*

Phoretic associations. A large number of emerging adults had mites (presumably phoretic) upon their ventral surfaces. Although some of these are known to be predaceous upon other arthropods, none was ever observed to feed upon the eggs or other instars of *Polygraphus rufipennis*, as has been noted for the genus *Tarsonemoides* (Acarina: Tarsonemidae), which preys upon the eggs of the genus *Ips* (Coleoptera: Scolytidae). Following is a list of the mites (Acarina, Acari) found on the ventral surfaces, near the coxae of adult *Polygraphus rufipennis*: Bdellidae—*Hoploscirus lapidaria* (Kramer). Ceratozetidae—*Diapterobates numerosus* (Sellnick). Cheyletidae—*Paracheyletia virginiensis* (Baker). Pyemotidae—*Pyemotes* sp. near *herfsi* (Oudemans), *Pyemotes* sp. near *scolyti* (Oudemans). Tyroglyphidae—*Histiogaster arborsignum* Woodring. Uropodidae—*Leiodinychus* sp.

Of 250 beetles dissected in a search for nematode parasites, only one male and one female had a large number of nematodes lying under the bases of the elytra. The nematodes were larval forms of either *Bursaphelenchus* or *Ektaphelenchus*. These larvae are non-parasitic and are presumably phoretic on the adult beetle. The adult nematodes are free-living in the frass and boring dust of bark beetle galleries.

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The Genus *Euphorbia* of the High Plains and Prairie Plains of Kansas, Nebraska, South and North Dakota

By

JAMES W. RICHARDSON[1]
Botany Department
University of Kansas

ABSTRACT

The attributed difficulty, confusion and recent advances in taxonomy that have occurred in the genus *Euphorbia* in the last few years make a revisional study advisable. Due to the lack of a recent taxonomic treatment for the area of the Great Plains and Prairies, the study was initiated to bring the status of the genus in this area up to date and to indicate some of the existing problems still to be solved in certain groups. Collections for herbarium material were made throughout Kansas, Nebraska, North and South Dakota and adjacent areas during the period of study. In addition, material from most of the major herbaria of the study area was examined. Keys to 4 subgenera, 21 species, and 2 varieties are provided as well as a diagnosis for the genus and each species. Synonomy for each is provided and each species and variety includes a description of habitat, distribution with accompanying maps, illustration of habit and/or seeds, and general discussion of taxonomic disposition.

INTRODUCTION

The Linnaean genus *Euphorbia* is the largest of the approximately 283 genera of the family Euphorbiaceae and contains an estimated 1600 species. It is probably one of the most broadly inclusive genera in modern usage. It consists of an assemblage of herbs, shrubs and trees from the subtropical to warm temperate regions of the world.

The attributed difficulty, confusion and recent advances in taxonomy that have occurred in this genus in the last few years make a revisional study advisable. Due to the lack of any recent taxonomic treatment for the area of

[1] Present address: Biology Department, Wisconsin State University, River Falls, Wisconsin.

the Great Plains and Prairies, this study was initiated to bring the status of the genus in this area up to date and to indicate some of the existing problems still to be solved in certain groups.

The genus Euphorbia in the High Plains and Prairie Plains of Kansas, Nebraska, North and South Dakota includes 21 species and two varieties for a total of 23 taxa.

Keys to subgenera, species, and varieties are provided as well as a diagnosis for the genus and each species. Synonomy for each is provided and each species and variety includes a description of habitat, distribution with accompanying maps, illustration of habit and/or seeds, and general discussion of taxonomic disposition.

MATERIALS AND METHODS

Field Studies: Collections for herbarium material were made throughout Kansas, Nebraska, North and South Dakota during the summers of 1965 and 1966. In many cases, collections were made in areas adjacent to the four state region for comparison purposes.

Herbarium Studies: In addition to personal collections and those at The University of Kansas (KANU), specimens were borrowed from the herbaria at the State University of Kansas (KSC) in Manhattan, University of South Dakota (SDU) in Vermillion, North Dakota State University (NDA) at Fargo and Southern Methodist University (SMU) in Dallas, Texas. Specimens in the herbaria at the University of Nebraska (NEB) and the Missouri Botanical Gardens (MO) were also studied.

Morphological Studies: During the field studies, flowering, fruiting and leaf material of plants from over the entire area were preserved in vials of 40% alcohol for later use in character analysis. From preserved, herbarium, and a limited amount of fresh material available from seeds grown under greenhouse conditions, a careful analysis of 20 characters per plant was completed for each species in the genus over the area of this study.

ACKNOWLEDGMENTS

I am gratefully indebted to Dr. Ronald L. McGregor for suggesting this problem and his supervision throughout the study; to Dr. R. C. Jackson and Dr. R. H. Thompson who read this dissertation and added valuable comments; to Dr. Derek Burch, Missouri Botanical Gardens, for his invaluable comments and opinions on many aspects of the study; to the curators of the various herbaria from which specimens were borrowed; to NSF which supported a portion of this study through a Systematic and Evolutionary Biology Travel Grant from the University of Kansas; and finally to the author's wife, Jeanette, for her continued encouragement and assistance throughout the period of study.

TAXONOMY OF THE GENUS

From the beginning date of 1753, the genus *Euphorbia* has been the source of a considerable amount of controversy as to whether it should be kept in its broad sense or divided into various sections, groupings, genera, or subgenera. According to Croizat (1936), the problem is as old as the herbalists who saw a distinction between *Chamaesyce, Tithymalus, Euphorbium* and *Peplis* but whose distinctions were rejected by Linnaeus in all his works.

The first revision of the entire genus was the work of Boissier (1862). During this same period, Dr. George Engelmann had done a large amount of work on the genus in North America and apparently had a monograph of his own in preparation. Engelmann, however, sent both notes and specimens to Boissier who incorporated many of them in his work (Norton, 1900).

A second major survey of *Euphorbia* was that of Pax and Hoffmann (1931) who combined all proposed genera but did not identify them beyond indicating that they belonged to the large diverse genus *Euphorbia*. Their classification indicated the division of the genus into nine sections with an estimated 1600 species.

Various other workers in the genus have attacked the problem in one of several ways. Sherff (1940) considered generic segregations impossible, while Norton (1900), Wheeler (1941), and many local floristic workers have divided the genus into sections or subgenera. Small (1933), Croizat (1936), Dressler (1961), and Burch (1966) have chosen to divide the complex into several separate genera, with Perry (1943) also suggesting that the complex could be broken up into several genera based on chromosome number, size and certain morphological differences.

Major works to include our area are those of Norton (1900) and Wheeler (1941). However, these men included only the species of a specific subgenus and not the entire genus. The only work to include all members of the genus *Euphorbia* (as treated in this paper) was that of Rydberg (1932) who divided the genus into six genera with a total of 24 species for our area. Other investigators have worked primarily at the level of state or regional floras such as the floras of Kansas (Gates, 1940), Nebraska (Winter, 1936), South Dakota (Winter, *et al.*, 1959), and North Dakota (Stevens, 1963).

During the course of this study, it became apparent that the problem of whether to treat the genus in its entirety or split it into several genera is still one to be conjectured and discussed for years. The problem may only be answered when a world-wide monograph has been completed to determine the true relationships and status of the taxa involved. Consequently, in this work I have followed the more-or-less classical approach and recognized the rather distinct groupings as subgenera under the very diverse genus *Euphorbia*.

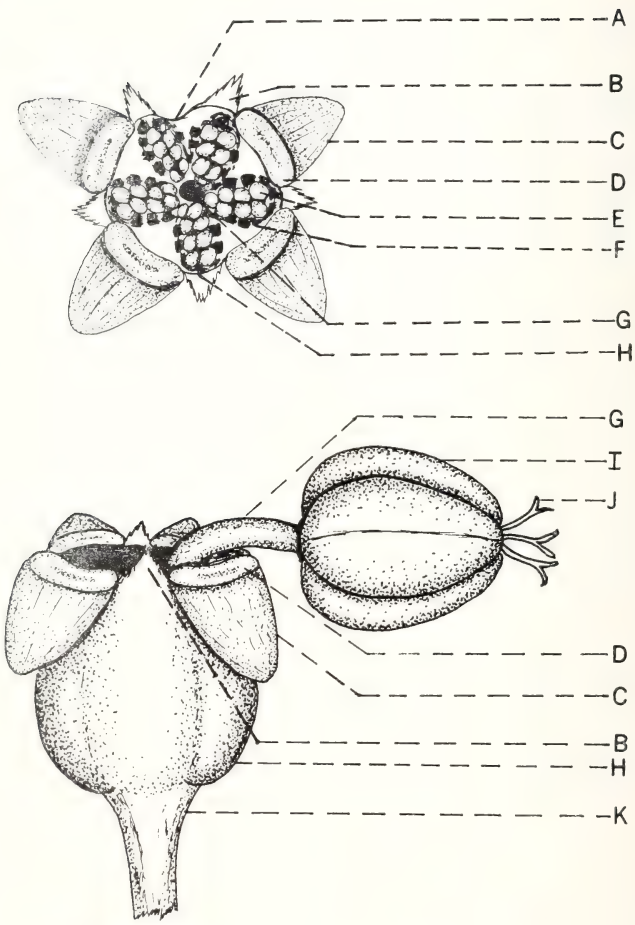


Fig. 1

FIG. 1. Subgenus *Chamaesyce* only. Upper. View of cyathium from above with capsule removed.

Lower. Side view of cyathium. A. Interval of reduced or absent 5th gland, gynophore usually recurved through interval. B. Lobe of involucre. C. Appendage. D. Gland. E. Staminate flower. F. Bracteole. G. Pedicel of pistillate flower (gynophore). H. Involucre. I. Developing capsule. J. Style. K. Peduncle.

GENERIC DIAGNOSIS

Annual, rarely biennial, or perennial, herbaceous; leaves simple, alternate, opposite or whorled, base equal to strongly unequal; inflorescence cymose, with either umbelliform branching and bearing a solitary "flower" at the summit of di- or trichotomous rays, or with a central terminal cyathium suppressed with branching more lateral; flowers monoecious, borne in a cupuliform structure (cyathium); the group of flowers surrounded by calyx-like involucre, bearing on its summit 1-5 nectariferous glands alternating with small foliaceous lobes, glands with or without colored petaloid appendages; one of glands usually absent or modified, its space occupied by an arching gynophore; staminate flower reduced to 1 stamen, naked, borne on filament-like androphore, arranged in fascicles from base of involucre with 1 to several flowers per fascicle, each with a single free or adnate basal bracteole; pistillate flower 1, pedicellate, naked, with rudimentary 3-lobed calyx at base of 3-locular sessile ovary, pedicel elongating and exerted, usually reflexed at maturity; styles 3, emarginate to distinctly bifid; capsule 3-celled, 3-seeded; seeds with or without caruncle, smooth to variously sculptured, with gelatinous coat of varying thickness. (See Fig. 1)

This diagnosis applies only to species incorporated in this paper.

ARTIFICIAL KEY TO SUBGENERA OF *Euphorbia*

1. Glands of cyathia with petaloid appendages.
   2. Leaves all strictly opposite, bases usually strongly inequilateral; stipules well developed ..... I *Chamaesyce*
   2. Leaves alternate, opposite, or whorled, bases symmertical; stipules absent or glandlike ..... II *Agaloma*
1. Glands of cyathia without petaloid appendages, lobed, crescent shaped, or entire.
   3. Glands usually 1 or 2, cup shaped with inflexed margin ..... III *Poinsettia*
   3. Glands 4 or 5, flat or convex, entire or crescent shaped ..... IV *Esula*

I. SUBGENUS *CHAMAESYCE* Raf., Amer. Mo. Mag. 2: 119. 1817. Type: *Euphorbia supina* Raf., designated by Wheeler, A miscellany of New World Euphorbiaceae—II. Contr. Gray Herb. 127: 59 footnote 2. 1939. For synonymy see Wheeler (1941, 1943).

1. Capsules glabrous.
   2. Plants perennial, leaf bases usually slightly cordate ..... 1. *E. fendleri*
   2. Plants annual, leaf bases usually oblique.
      3. Stipules united into a prominent, white, glabrous scale; typically rooting at nodes ..... 2. *E. serpens*
      3. Stipules not united; not rooting at nodes.
         4. Tips of stems and base of leaves variously pubescent ..... 3. *E. nutans*
         4. Plants completely glabrous throughout.
            5. Leaves entire.
               6. Mature capsule 2 mm or less long; plants prostrate to semi-

prostrate; appendages of glands small, less than 0.5 mm long ..... 4. *E. geyeri*

6. Mature capsule 2 mm or less long; plants porostrate to semiprostrate; appendages ofg lands small, less than 0.5 mm long ..... 4. *E. geyeri*

5. Leaves variously serrate.

7. Seeds with 3-7 prominent transverse ridges. ..... 6. *E. glyptosperma*

7. Seeds smooth to wrinkled or rugulose, not transversely ridged ..... 7. *E. serpyllifolia*

1. Capsules variously pubescent.

8. Plants perennial, leaf bases truncate to slightly cordate ..... 8. *E. lata*

8. Plants annual, leaf bases usually oblique.

9. Seeds with narrow sharp transverse ridges; capsule primarily pubescent on angles ..... 9. *E. prostrata*

9. Seeds with low broad ridges, punctately pitted, to nearly smooth, mottled or roughened; capsule rather uniformly pubescent.

10. Seeds pitted or mottled, not transversely ridged, base truncate and concave ..... 10. *E. stictospora*

10. Seeds roughened or with low broad transverse ridges, base rounded, not concave.

11. Seeds nearly smooth, granular to punctately roughened; styles 0.5-0.7 mm long; stems occasionally rooting at nodes; leaves typically orbicular to ovate, emarginate to rounded at apex ..... 11. *E. humistrata*

11. Seeds with low transverse ridges, not roughened; styles ca. 0.4 mm or less (rarely to 0.6 mm) long; stems never rooting at nodes; leaves linear to oblong, typically acute at apex ..... 12. *E. maculata*

II. SUBGENUS *AGALOMA* (Raf.) House, N.Y. State Mus. Bull. 254: 471. 1924 based on *Agaloma* Raf. Type: *Euphorbia corollata* L., assigned by Rafinesque, Aut. Bot. 95. 1840.

Agaloma Raf., Fl. Tellur. 4. 116. 1838.
Lepadena Raf., Fl. Tellur. 4: 113. 1838. Type: *L. leucoloma* (Raf.) Raf.; based on *Euphorbia marginata* Pursh.
Dichrophyllum Klotzsch & Garcke, Monatsb. Akad. Berlin, 249. 1859. Type: *Euphorbia marginata* HBK.
Zygophyllidium (Boiss.) Small, Fl. Se. U.S. 715. 1334. 1903. Type: *Zygophyllidium hexagonum* (Nutt) Small; based on *Euphorbia hexagona* Nutt.
For additional synonymy see Wheeler (1943).

1. Cauline leaves all opposite, petiolate, linear to narrowly lanceolate ..... 13. *E. hexagona*

1. Cauline leaves alternate, sessile to subpetiolate, oval to oblong.

2. Plants annual; glands 4; mature capsules densely pubescent; leaves and bracts of inflorescence with broad, white to pink petaloid margins ..... 14. *E. marginata*

2. Plants perennial from deep subterranean root stock, glands 5; mature capsule glabrous; leaves and bracts of inflorescence reduced and without petaloid margins ..... 15. *E. corollata*

III. SUBGENUS *POINSETTIA* (Graham) House, N.Y. State Mus. Bull. 254: 473. 1924, based on genus *Poinsettia* Graham, New Philos. Journ. 20: 412. 1836. Type: *Poinsettia pulcherrima* (Willd.) Graham, l. c.; based on *Euphorbia pulcherrima* Willd. ex Klotzsch in Otto & Dietr., Allg. Gartenz. 2: 27. 1834.

Cyathophora Raf., Fl. Tell. 4: 117. 1838, not *Cyathophora* S. F. Gray, 1821. Type: *Cyathophora heterophylla* (L.) Raf., based on *Euphorbia heterophylla* L.
For additional synonymy see Wheeler (1943).

1. Leaves relatively uniform in shape throughout; cauline leaves all opposite, hairy on both surfaces; floral bracts green and typically mottled with red spots, usually cream colored basally ..... 16. *E. dentata*
1. Leaves with two distinctly different shapes; cauline entire and linear to narrowly lanceolate, all or mostly alternate, pubescent below primarily along veins, glabrous above; floral leaves and bracts usually lobed or panduriform, green, typically red basally ..... 17. *E. cyathophora*

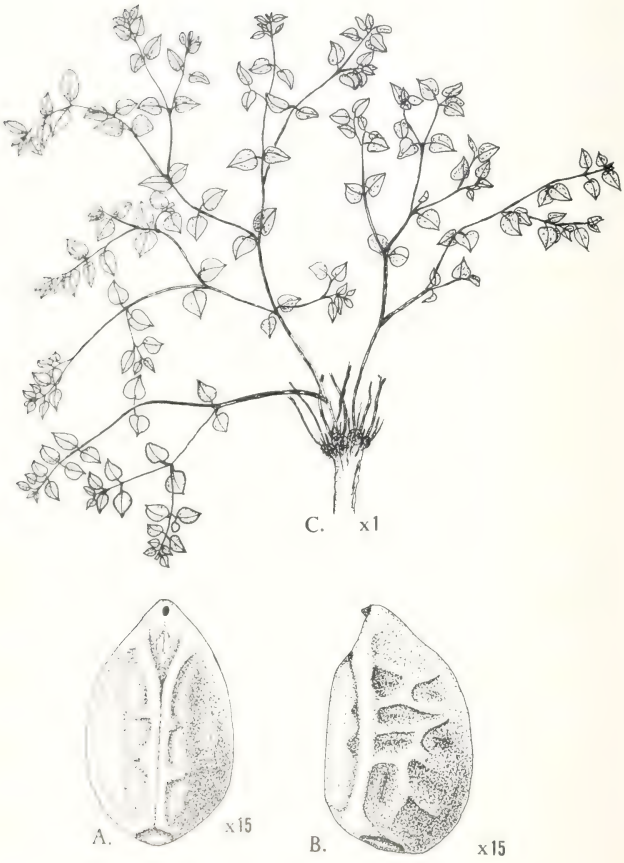
IV. SUBGENUS *ESULA* Pers., Syn. Pl. 2: 14. 1806. Type: *Euphorbia peplis* L.
Euphorbia sect. Tithymalus of various authors.
Tithymalus of various authors.
Galarhoeus Haw. Synopsis plantarum succulentarum. 143. 1812. Type: *Galarhoeus helioscopia* (L.) Haw.; based on *Euphorbia helioscopia* L.
For additional synonymy see Wheeler (1943).

1. Ovary and capsule with conical to cylindrical papillae; seeds reticulate and thick-lenticular; glands transversely oval ..... 18. *E. spathulata*
1. Ovary and capsule smooth to faintly roughened along suture line of capsule; seeds smooth to slightly roughened and globose ovoid; glands with prominent horns and crescent-shaped.
   2. Style and stigma of young exerted ovary very long and equaling or exceeding immature capsule in length ..... 19. *E. podperae*
   2. Style and stigma of young exerted ovary short and not exceeding immature capsule in length.
      3. Cauline leaves linear, not over 3 mm wide ..... 20. *E. cyparissias*
      3. Cauline leaves broadly ovate, 4 mm or more wide ..... 21. *E. robusta*

1. **Euphorbia fendleri** T. & G., Rep. Expl. & Surv. Miss. R. to Pacific Ocean 2 (4): 175. 1855. Type: Santa Fe, New Mexico, May 4-July 18, 1847, *Fendler 800* (NY: isotypes G, MO!).
E. greenii (Millsp.) Rydb., Fl. Pr. Plains, 517, fig. 350. 1932.

Perennial; stems prostrate to erect, 3-15 cm long, glabrous; leaves glabrous, lanceolate, ovate, to ovate-orbicular, 3-7 mm long, 2-8 mm wide, apex acute to obtuse, base oblique to slightly cordate, margin entire; petiole 1-2 mm long, concave on upper surface; stipules glabrous, to 1 mm long, free to slightly united basally, segments narrowly lanceolate to linear; cyathia with peduncles 1.0-1.5 mm long, glabrous; involucres turbinate, 1-2 mm long, glabrous out-

Fig. 2



Euphorbia fendleri T. & G.

[illegible] A. Ripened [illegible] of seed. B. Side view of seed with raphe on [illegible] Hilum at point.

side, glabrous to densely pubescent inside at summit; lobes broadly caudate to acuminate, slightly pubescent on margins, equaling or exceeding the glands in length; glands discoid to concave, red to orange-red in color; appendages white to reddish, minute and much shorter than width of gland, entire to crenulate; bracteoles fused into a single appendage, apex laciniate, fused basally with involucre, glabrous to pubescent, slightly emerging from involucre; staminate flowers 2-5 per fascicle, 13-25 per involucre; gynophore glabrous and soon exerted, straight to sharply reflexed, 5-6 mm long at maturity; styles to 0.5 mm long, bifid for ½ entire length, glabrous, thickened; mature capsule 1.5-2.5 mm long, glabrous, usually only 1-2 seeds produced per capsule; seeds 1.0-1.7 mm long, 0.7-1.0 mm wide, ovate-oblong, ventral facets concave, smooth or with few low irregular transverse ridges, dorsal facets plain to convex with several prominent irregular transverse ridges and furrows, coat white to tan. Fig. 2.

Habitat: Sandy to rocky, undisturbed, short grass prairies and to a limited extent stabilized sand dunes.

Range: Records from southwestern portions of Kansas, Nebraska panhandle, and South Dakota. Map 1.

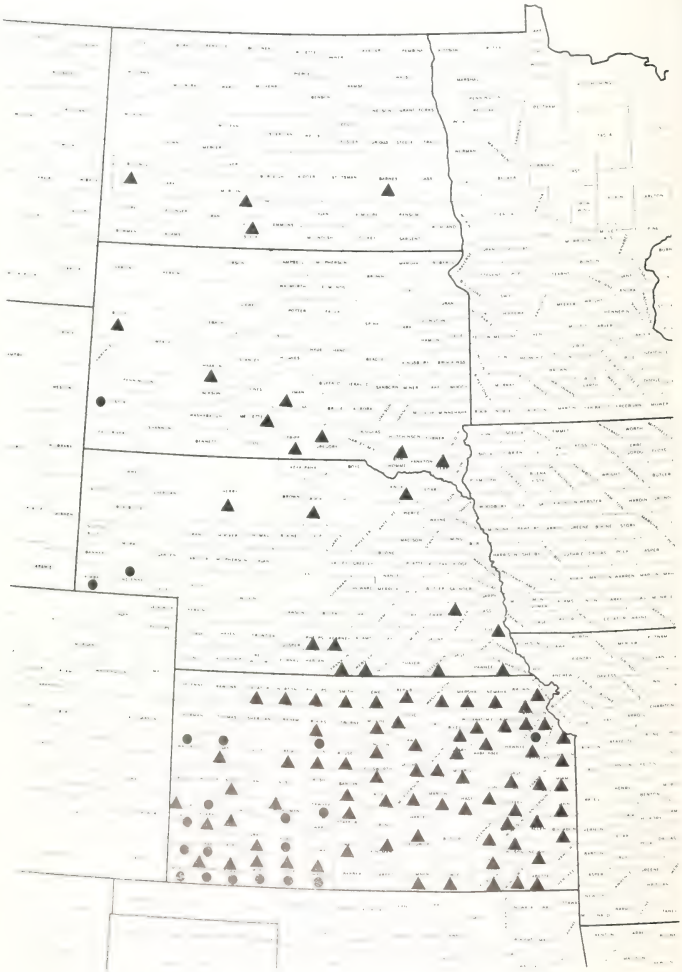
A collection in KSC of *E. fendleri* from Oskaloosa, Jefferson Co., Kansas, *Kellerman s.n.*, bears the notation, "Loc. questionable." Although it is possible the collection site is correct, it is entirely out of the range of the species and most likely, inaccurately labeled.

A rather unusual tendency to produce only one or two seeds was noticed in virtually all material examined. Many capsules with only one developed seed had the other two cells either without seed and reduced or with seeds only partially developed and dried or shriveled. Rarely did any of the capsules contain three developed seeds but, if three, I found only one, rarely two, would germinate in the greenhouse.

2. **Euphorbia serpens** HBK., Nov. Gen. et Sp. 2: 52 (quarto), 41 (folio). 1817. Type: Cumana, Venezuela, *Bonpland 407* (P; photograph G, fragment F).

Annual, stems prostrate, 2-40 cm long, glabrous, internodes up to 4 cm, becoming progressively shorter and more leafy late in season, rooting extensively at nodes on older portions of plant; leaves glabrous, orbicular to obvate-orbicular, 2-10 mm long, 2-7 mm wide, apex obtuse or retuse, base subcordate to oblique, unequal side with lobe up to 1 cm long; petiole to 1 mm long, terete; stipules glabrous, to 1 mm long, fused into a white, membranous scale with apex deeply lacerate, incised or ciliate; cyathia with peduncles 2-3 mm long, glabrous; involucres turbinate, 1.0-1.5 mm long, glabrous both outside and inside; lobes lanceolate, glabrous, exceeding the glands in length; glands transversely oblong, yellowish green in color; appendages white to rose-pink, minute (rarely absent) to slightly longer than width of gland, entire to crenate or lobed; bracteoles fused forming a single appendage,

Map 1



entire or parted, glabrous to slightly pubescent at apex, extending only to summit of involucre; staminate flowers usually 1-3 (rarely none) per fascicle, 3-12 per involucre; gynophore typically reflexed at maturity; ovary glabrous; styles 0.2 mm long, bifid ½ entire length, slightly clavate; mature capsules 1.0-1.5 mm long, 1.5 mm wide, glabrous; seeds 0.9-1.3 mm long, 0.5-0.8 mm wide, plump, oblong to ovoid, angles rounded, facets smooth, coat white to brown. Fig. 3.

Habitat: plants of moist alluvial or rich sandy soils of roadsides, waste areas, eroded areas in prairies, and woodlands. In general *E. serpens* is one of the pioneer plants which tends to become established in areas of high disturbance and is, therefore, quite commonly found along newly constructed roads, graded roadsides, and in areas where periodic flooding occurs. Rooting at the nodes gives the plant good soil retaining ability. A general trend of increasing seed length from east to west was noticed. Seeds from the eastern portion tended to be shorter (0.9-1.0 mm), with a very gradual increase in seed length to about 1.1-1.3 mm in the western portions of the range.

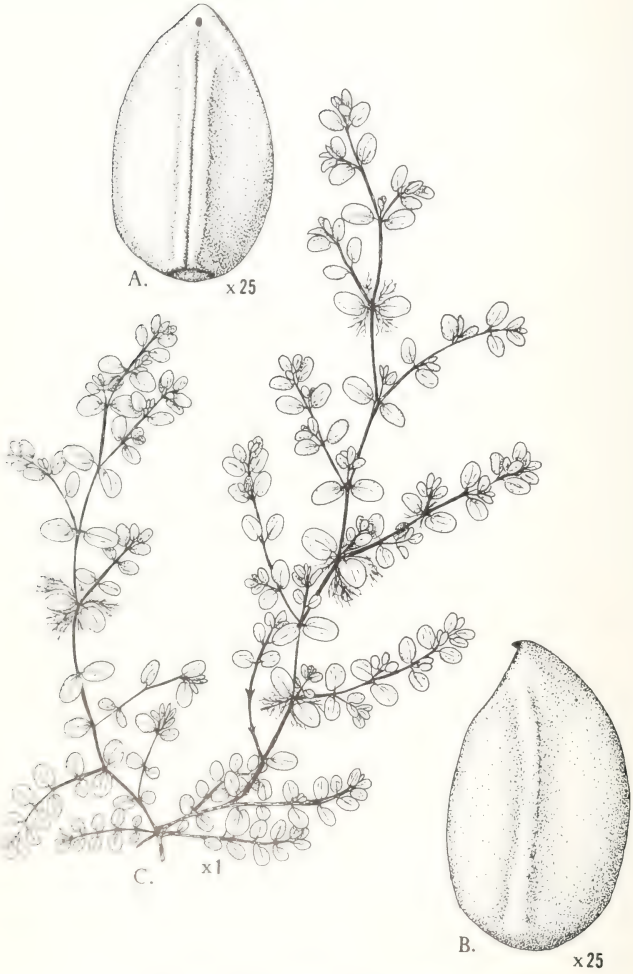
Range: Scattered in southern North and South Dakota, north central and southeastern Nebraska, with records over most of Kansas except for the extreme northwestern portion. Map 1.

A variable species as to appendage size and stipules. Although in the key the fused stipules separates *E. serpens* from the other glabrous species in our area, it was found that rarely a few specimens will show stipules that are virtually free, particularly on the younger portions of the plants. However, the features of the seeds, rooting at nodes and shape of the leaf (in addition to stipules) tend to separate this species very adequately.

3. **Euphorbia nutans** Lag., Gen. et. Sp. Pl., 17. 1816. Type: "Habit. [at] in N. [ova] H. [ispaniola]"
   E. preslii Guss., Fl. Sic. Prod. 1: 539. 1857. Type: Palermo, Italia, Todaro (Praha; fragment F).
   E. maculata L. (*sensu* Wheeler).

Annual; stems decumbent to erect, 5-75 cm tall, tomentose primarily on younger portions of plant at nodes and in lines on stem, internodes 1-6 cm long; leaves long villous to pilose, mainly at base, both above and below, broadly lanceolate, ovate, oblong or falcate, typically red mottled above and below, commonly solid red in color below, 5-40 mm long, 3-15 mm wide, apex obtuse, base oblique, unequal side with lobe up to 1.5 cm long, margin prominently serrate; petiole 2 mm or less long, slightly concave on upper surface; stipules triangular-acuminate to 1.5 mm long, glabrous or with pubescent margin, fused basally with apex deeply incised to laciniate, cyathia with pedicels 0.5-5.5 mm long, glabrous; involucres narrowly campanulate, 0.5-0.7 mm long, glabrous outside, pubescent inside at summit of involucre; lobes lanceolate to laciniate, to ca. 1 mm long and exceeding glands; glands elliptic to rotund, concave, green, stipes 1 mm or less long, pubescent; appendages

Fig. 3



Euphorbia serpens HBK

Fig. 3. Euphorbia serpens. A. Ventral view of seed. B. Side view of seed with raphe

white to slightly pink, to 1.5 mm long, to 1.7 mm wide, wider than gland, entire to slightly lobed at apex; bracteoles fused to sides of involucre for ¾ their length and forming a partition between fascicles of staminate flowers, apex entire or with several filiform to linear segments, pubescent along margin; staminate flowers 1-6 per fascicle, 5-28 per involucre; gynophore strongly reflexed at maturity; ovary glabrous; styles 0.6-2.5 mm long, bifid for less than ½ entire length, spreading with tips reflexed; mature capsules 1.6-2.0 mm long, 2.0-2.7 mm wide, glabrous; seeds 1.1-1.5 mm long, 1.0 mm wide, elliptic-ovoid, angles rather sharp, facets flat to slightly convex, transversed by several low irregular ridges, coat black to dark brown with angles usually lighter in color. Fig. 4.

Habitat: Generally considered a weed in waste areas, grasslands, roadsides and flood plains of rivers. The collections from the western and northern limits of the range indicate that the species is adapted to relatively moist sandy soils.

Range: Primarily the eastern two-thirds of Kansas, eastern one-half of Nebraska, southeastern portions of South Dakota with one record from eastern North Dakota (Cass Co.). The latter gives a collection note for location as railroad near Fargo which would indicate that the plant was adventive and not natural in occurrence. In addition, no other collections have been seen of this species from North Dakota. The collections from extreme western Kansas (Wallace & Greeley counties) lack any habitat information and it is difficult to make any assumptions as to whether they were native or introduced. Also, Harrington (1964) does not list this species from Colorado and no other collections have been seen from this general area which would lead one to believe them to be introduced and not native. Map 2.

A vast amount of controversy has centered around the correct name which should be applied to this species. In general, the names most often encountered are *E. maculata* L., *E. preslii* Guss., and *E. hypericifolia* L. The problem appears to stem from a series of four species in America which are all very similar in general habit. According to Burch (1966), the problem is the application of the name *E. hypericifolia* which has been used for both a northern plant (the plant found in our area) and a tropical or subtropical plant. Also to be considered is the name *E. maculata* L. as applied by Wheeler (1939) and the subsequent application of this name by most authors. For details on the application of *E. maculata,* see the discussion under this species.

As stated by Burch *(loc. cit.),* the usage of *E. hypericifolia* has become so firmly established for the tropical or subtropical species that any change would cause more confusion; and the application of this name should be continued. This, however, still leaves the name for the northern entity to be decided. Since most authors accept Wheeler's application of *E. maculata* there seems to be no problem. However, Burch has indicated that the sheet

Fig. 4

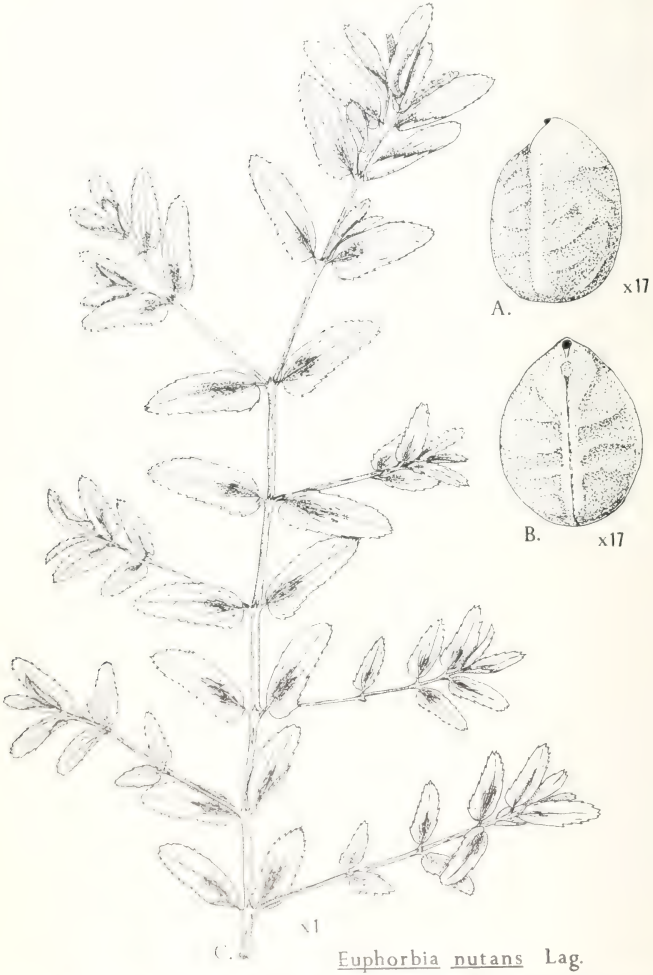


Fig. 4. *Euphorbia nutans*. A. Ventral view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

used as type for *E. maculata* (*sensu* Wheeler) probably was not in Linnaeus' possession until after publication of *Species Plantarum*. On this and other evidence, Burch rejects *E. maculata* and proposes the name *E. nutans* Lag. for our species.

As indicated by many workers, the problem with the name to apply to this entity is one of confusion and in many cases misinterpretation. With this in mind, and based on the latest findings by Burch, however, I have excepted his usage and used the name *E. nutans* for the entity that occurs in our range.

4. **Euphorbia geyeri** Engelm. in Engelm. & Gray, Bost. Journ. Nat. Hist. 5: 260. 1845. Type: Beardstown, Cass County, Illinois, Aug., 1842, *C. A. Geyer* s.n. (MO!)

Annual; stems prostrate, rarely ascending 5-30 cm long, glabrous; leaves glabrous, oblong to oblong-ovate, 4-12 mm long, 2-5 mm broad, apex obtuse to emarginate, base oblique to slightly cordate, unequal side with lobe up to 0.5 mm long, margin entire, petiole glabrous, 1-2 mm long; stipules glabrous, to 2 mm long, basally united, dividing into 2-5 linear to linear-lanceolate segments; cyathia with peduncles to 2 mm long, glabrous; involucres campanulate, to 1 mm long, glabrous outside, pubescent inside at summit; lobes lanceolate-acuminate, sparingly pubescent along margin; glands oval to elliptic, usually cupped or folded, reddish in color at maturity; appendages white to reddish, wider than gland, to 0.5 mm long, ovate to obovate, entire, apex rounded to acute; bracteoles forming a partition between fascicles of stamens, fused basally and to involucre for ½ entire length, dissected above into many pubescent linear segments, equalling or slightly exceeding summit of involucre; staminate flowers 1-5 (rarely 6) per fascicle, 5-27 per involucre, gynophore glabrous and soon exerted and reflexed, 2-4 mm long at maturity; ovary glabrous; styles 0.2-0.5 mm long, bifid for ⅓ entire length, glabrous, thickened to slightly clavate; capsule 1.5-2.0 mm long, 2-3 mm wide, glabrous, sharply 3 lobed, wider below equator; seeds 1.3-1.7 mm long, 0.7-1.2 mm broad, broadly subtriangular to ovate; smooth, facets convex, angles low and rounded, white to light brown or white with brown mottling. Fig. 5.

Habitat: The range of this species is definitely associated with sandy conditions from dunes (usually stabilized), sandhills to sandy waste areas and barrens.

Range: Records from southcentral and southwestern Kansas, the sand hills region of Nebraska and South Dakota, and scattered sandy areas in North Dakota. Map 2.

Wheeler (1941) gives the staminate flower number as 5-17 per cyathium. Examination of our material, however, revealed the flower number went much higher (as high as 27) and appeared rather consistently over our range. Examination of material from regions adjacent to ours (Minnesota, Okla-

Map 2

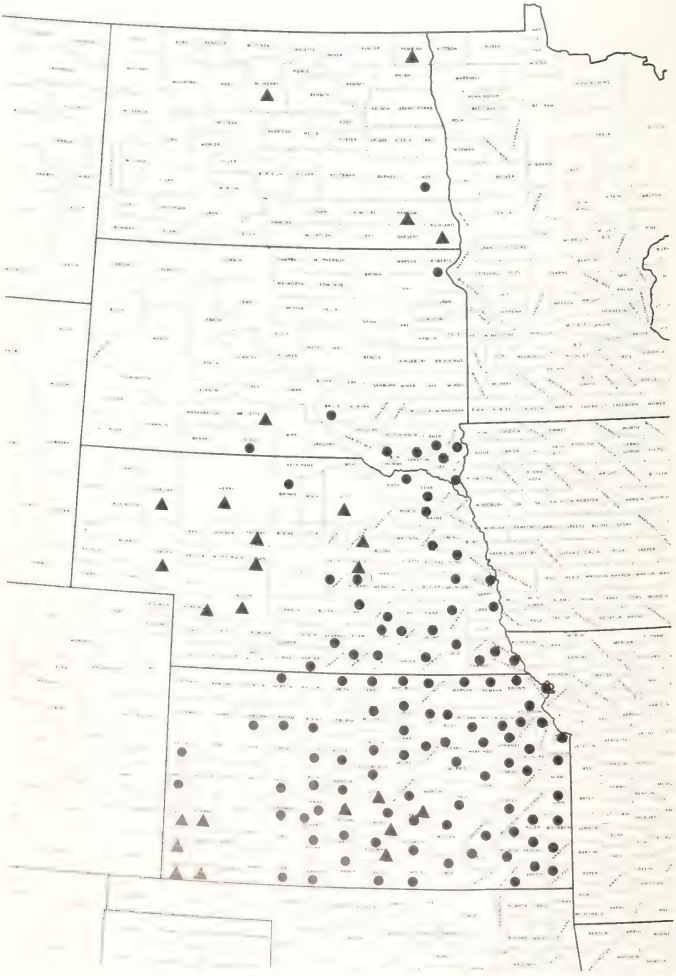
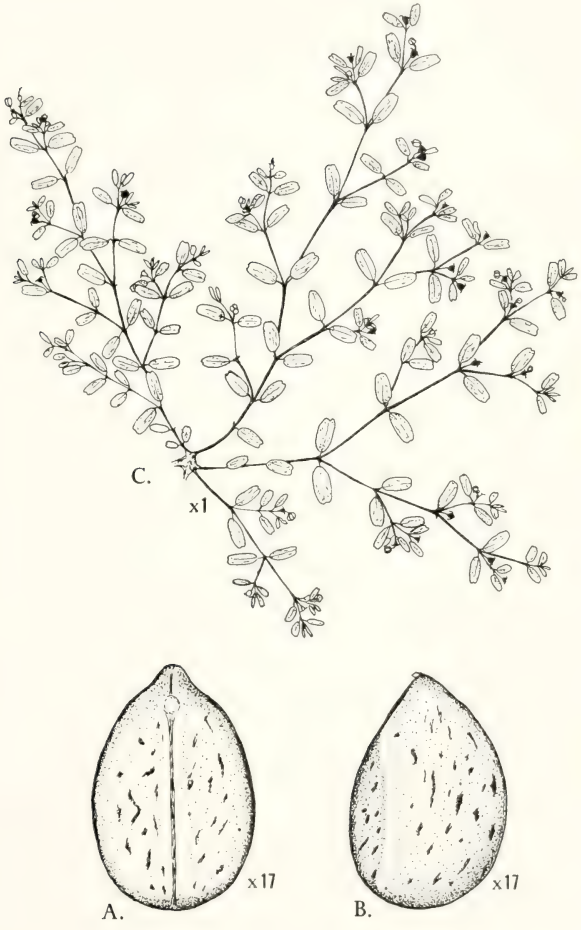


Fig. 5



Euphorbia geyeri Engelm.

FIG. 5. *Euphorbia geyeri*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

Journ. and Texas) revealed that the number still, in most cases, was higher than that listed by Wheeler.

The species most often confused with this one is *E. glyptosperma* Engelm. However, the entire leaves and smooth seeds easily separate *E. geyeri* Engelm. from *E. glyptosperma* Engelm. which has serrate leaves and seeds with prominent transverse ridges.

5. **Euphorbia missurica** Raf., Atlantic Journ. 1. 146. 1832.

Annual; stems decumbent to erect, 0.5-9.0 cm long, glabrous, internodes 0.5-6.0 cm long; leaves glabrous, linear to elliptic, 0.5-3.0 cm long, 2-10 mm wide, apex obtuse acuminate to emarginate, base symmetrical to slightly inequilateral; petiole 1-3 mm long, terete; stipules glabrous, linear to triangular, fused basally, apex dissected into 1-5 linear to linear-lanceolate segments; cyathia with pedicels 1-10 mm long, glabrous; involucres campanulate, 1.5-2.0 mm long, glabrous outside, pubescent inside at summit; lobes triangular, glabrous to slightly pubescent inside and along margin, exceeding the glands in length; glands subcircular to transversely oblong, cupped or depressed; appendages white to pink or red, 0.5-2.5 mm long, 0.5-2.5 mm wide, wider than gland, entire, oblong to subcircular; bracteoles united basally, forming a partial partition around and between fascicles of staminate flowers, either reduced with apex dissected into 2-3 linear segments or large and highly dissected above, short hairs along margin of segments; staminate flowers 2-17 per fascicle, 10-76 per involucre; gynophore well-exerted and reflexed at maturity; ovary glabrous; styles 0.2-0.9 mm long, bifid for ½-¾ entire length; mature capsules glabrous, 2-3 entire length; mature capsules glabrous, 2-3 mm long, 2.5-3.5 mm wide; seeds 1.2-2.2 mm long, 1.0-1.4 mm wide, ovate to narrowly oblong, facets smooth and glossy or granular roughened to rugose with low irregular ridges or wrinkles, to shallowly pitted, coat solid white or mottled with dark brown spots.

Two varieties exist in our area and are distinguished as follows:

Key to Varieties

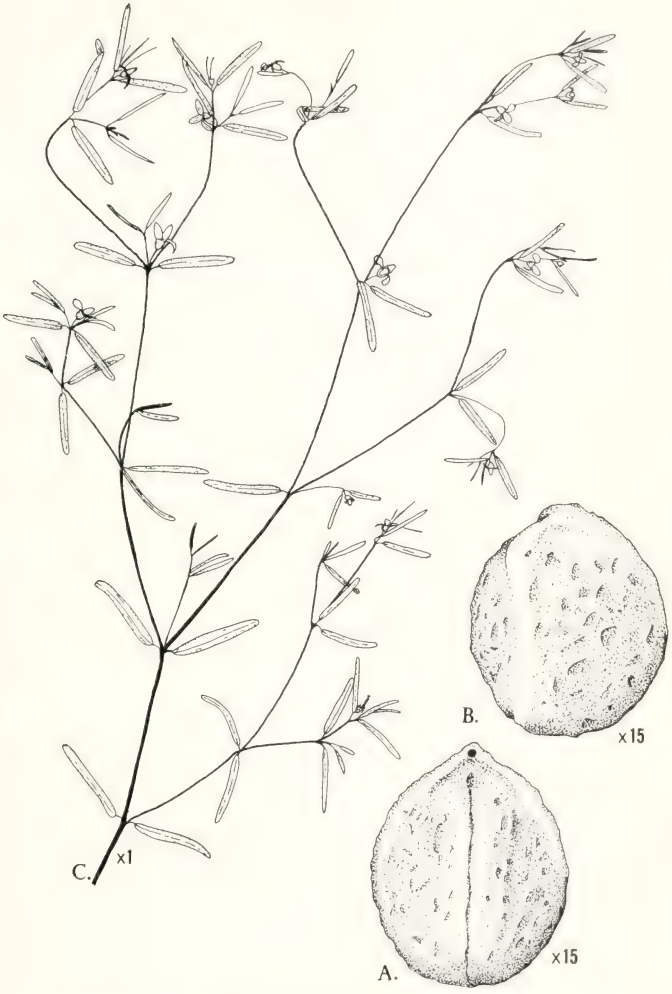
a. Plants erect; leaves 3.5 mm or less wide, linear to narrowly oblong; seeds 1.2-1.7 mm long, typically ovate, coat dull, granular and roughened to rugose or pitted, definitely angled ..... 5a. *E. missurica* var. *missurica*

a. Plants decumbent to ascending; leaves 2-10 mm wide, elliptic, to narrowly oblong; seeds 1.5-2.2 mm long, typically oblong coat, glossy and smooth, rarely angled ..... 5b. *E. missurica* var. *intermedia*

A tabular comparison of the two varieties follows:

var. *intermedia* (Fig. 7)	var. *missurica* (Fig. 6)
Decumbent to ascending	Erect

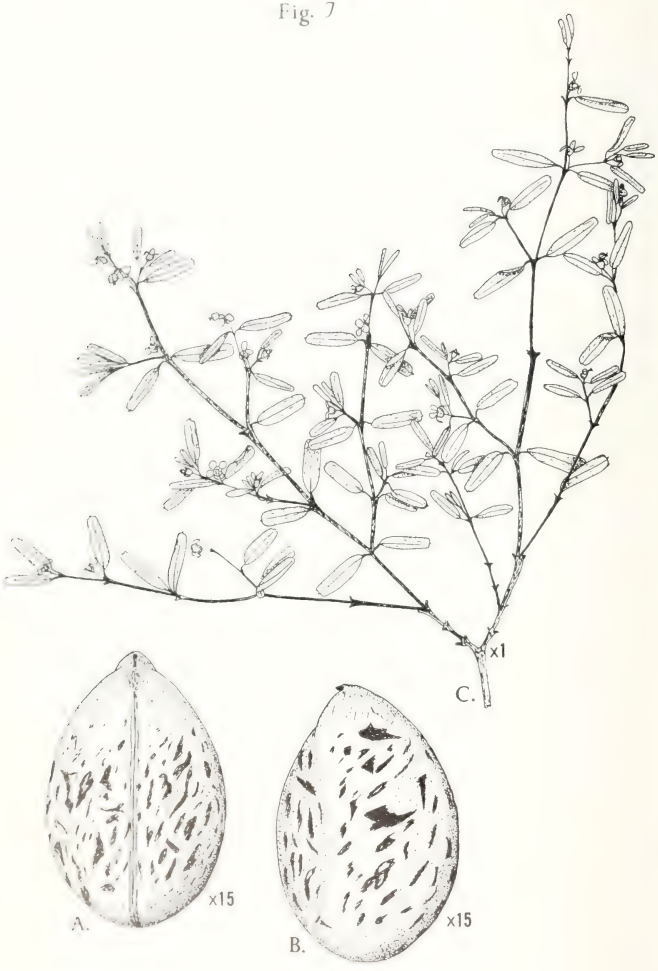
Fig. 6



Euphorbia missurica Raf. var. missurica

FIG. 6. *Euphorbia missurica* var. *missurica*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

Fig. 7



Euphorbia missurica Raf. var. intermedia (Engelm.) Wheeler

ar. *intermedia*. A. Raphial view of seed. B. Side view of

Stems firm and rather thick; ultimate branchlets stout	Stems delicate appearing; ultimate branchlets wiry, very slender
Leaves elliptic to narrowly oblong, 2.5-10.0 mm wide; apex usually obtuse	Leaves linear to narrowly oblong 0.5-3.5 mm wide; apex usually truncate
Peduncles 1-5 mm long, stout	Peduncles 1-10 mm long, slender
Cyathia tend to be clustered at tips of branches, involucres 1.7-2.0 mm long	Cyathia scattered, not clustered; involucre 1.5-2.0 mm long
Appendages typically broad and subcircular, 0.5-2.0 mm long and wide, usually at right angles to involucre, or if reflexed, typically not exceeding involucre in length	Appendages typically oblong, 1.5-2.5 mm long, 1.0-1.4 mm wide, usually reflexed and equaling or more typically exceeding involucre in length
Seeds narrowly oblong to ovate, 1.5-2.2 mm long, plump; coat glossy and smooth; angles low; rounded, barely discernible	Seeds broadly ovate, 1.2-1.7 mm long; coat dull, granular, roughened to rugose or shallowly pitted; seeds definitely angled

As can be seen from the comparison of the two varieties, a certain amount of overlapping does exist. In general, there are specimens which do not readily fall in one variety or the other; but by using multiple characters, specimens can still be assigned to one or the other variety. I found that when mature seeds were present, the assignment to a variety on the characteristics of the seed coat and shape easily separated the specimens and exhibited very little, if any, integradation.

5a. **E. missurica** Raf. var. **missurica**

E. petaloidea var. *nuttallii* Engelm. in Emory, U.S. & Mex. Bound. Surv. 2 (1): 185. 1859.
E. nuttallii (Engelm.) Small in Britton & Brown, Ill. Fl. No. U.S. & Can. 2: 371. 1897.
Chamaesyce missurica var. *calcicola* Shinners, Field & Lab. 17: 69. 1949. Type: Texas: Ellis Co.: 4 mi. north-northeast of Midlothian, Shinners 9367 (SMU!).
Euphorbia missurica var. *calcicola* (Shinners) Waterfall, Rhodora 54: 127. 1952.

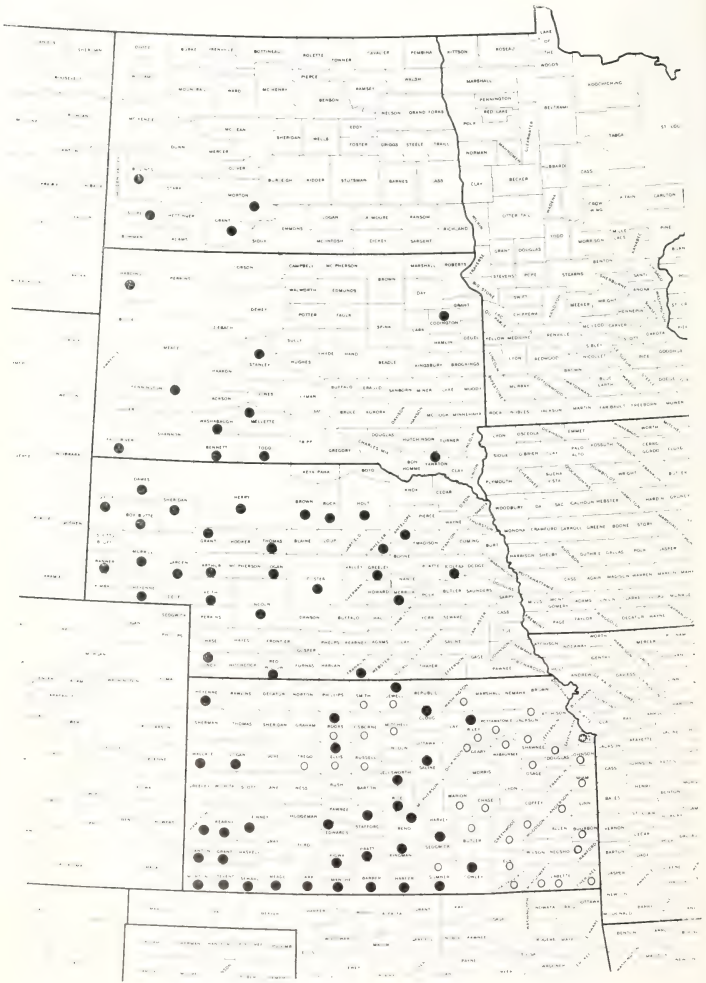
Habitat: Areas of moist grassland and flood plains to rocky, sandy, dry open prairies or occasionally along disturbed roadsides.

Range: The northern extension of the range of this variety appears to be Kansas and, at present, from the northcentral and eastern one-third of the state. This variety may very well be expected from the southeastern portions of Nebraska, but to date no collections have been seen to confirm this. Map 3.

Due to the confusion existing in the nomenclature and identification of the two varieties of *missurica*, a general discussion of both follows var. *intermedia*.

Shinners (1949 under the var. *calcicola*) indicates this variety, in Texas, from caliche or cretaceous chalk and limestone outcrops. In Kansas, however, due to a limited amount of collection data on herbarium sheets and

Map 3



personal collections of this variety, the habitat cannot be so restricted at this time. If one refers to a geologic map of Kansas, it can be seen that a series of counties (Jewell to Trego) contain Niobrara (Cretaceous) chalk. At the same time, it will be noticed that a series of collections of this variety also occurs in this area. Whether the collections were made from these areas of chalk is rather speculative. Future collections will more fully determine the habitat.

5b. **E. missurica** Raf. var. **intermedia** (Engelm.) Wheeler, Proc. Biol. Soc. Wash. 53: 11. 1940. Type: Fort Pierre, Standley Co., South Dakota, *Hayden* s.n. (MO!)

E. petaloidea Engelm., *in* Emory, U.S. & Mex. Bound. Surv. 2 (1): 185. 1859. Type: Forks of the Platte River, Lincoln Co., Nebraska, *Engelman* s.n. (MO!)

E. petaloidea nicolletii Engelm. *in* Emory, U.S. & Mex. Bound. Sur. 2 (1): 185. 1859. Type: Mouth of Powder River, Yellowstone, Prairie Co., *Hayden* s.n. (MO!)

Habitat: Generally associated with very dry, sandy soils, from sand dune areas to sandy, short, bunch grass prairies and roadsides.

Range: Western two-thirds of Kansas and Nebraska with collections scattered primarily in western one-half of South Dakota and southwestern portion of North Dakota. Map 3.

Wheeler (1940) published variety *intermedia* based on a specimen collected by Hayden in South Dakota. Although the specimen was sterile, the plant had the broad leaves typical of the form common throughout most of the great plains. Associated with broad leaves are the smooth glossy plump seeds, short peduncles, and rather robust appearance. However, in comparing these characters with those of the key to the varieties of *missurica* (Wheeler, 1941), it became apparent that portions of his key were reversed. The reversal became even more evident after examination of descriptions of synonyms listed by Wheeler and specimens annotated by him.

Consequently, if the broad-leaved, smooth-seeded form is var. *intermedia*, then the narrow-leaved, rough-seeded form is automatically var. *missurica* (*typica* of Wheeler). Hence, var. *missurica* (*typica* of Wheeler) is as follows: leaves linear, apex truncate, mostly emarginate; ultimate branchlets mostly more-or-less capillary; seeds mostly definitely angled, micropylar area obliquely truncate; peduncles up to 11 mm long, capillary.

Variety *intermedia* has leaves broadly oblong to linear, apex obtuse to slightly retuse; ultimate branchlets not capillary; seeds scarcely angled, micropylar area not markedly flattened and truncate; peduncles up to 4 mm long.

Shinners (1949) published a new variety *calcicola* from Texas, based on a narrow leaved form found in Ellis Co., Texas (*Shinners 9367*). After examining the type and several other specimens annotated as this variety, I found that var. *calcicola* corresponds to var. *missurica* and have reduced this variety to synonomy under var. *missurica*.

In the same publication, Shinners (1949) refers to a collection by J. Reverchon in which the original number (Curtiss, N. Amer. Plants 2468*) had been crossed out, and 2405* written beneath, with the name *Euphorbia arenaria* replaced by *E. zygophylloides*. A duplicate specimen of this same collection exists in the herbarium at KANU. Instead of the names and numbers being crossed out, however, a printed label has been placed over each entry and the number 2504* placed over 2468*, not 2405 as Shinners states.

6. **Euphorbia glyptosperma** Engelm. *in* Emory, U.S. & Mex. Bound. Surv. 2 (1): 187. 1859. Type: Fort Kearney on the Platte River, Kearney County, Nebraska, July, 1856, *H. Engelmann* s.n. (MO!)

E. glyptosperma Engelm. var. *tenerrima* Engelm. in Emory, U.S. & Mex. Bound. Surv. 2 (1): 187. 1859. Type: Pebbly bars the Nueces River, Texas, May 25, 1851, *C. Wright 1853* (MO!).

Chamaesyce glyptosperma Engelm. var. *integrata* Lunell, Amer. Midl. Nat. 3: 142. 1913. Type: Leeds, Benson County, North Dakota, Aug. 20, 1906, *J. Lunell 693* (MIN).

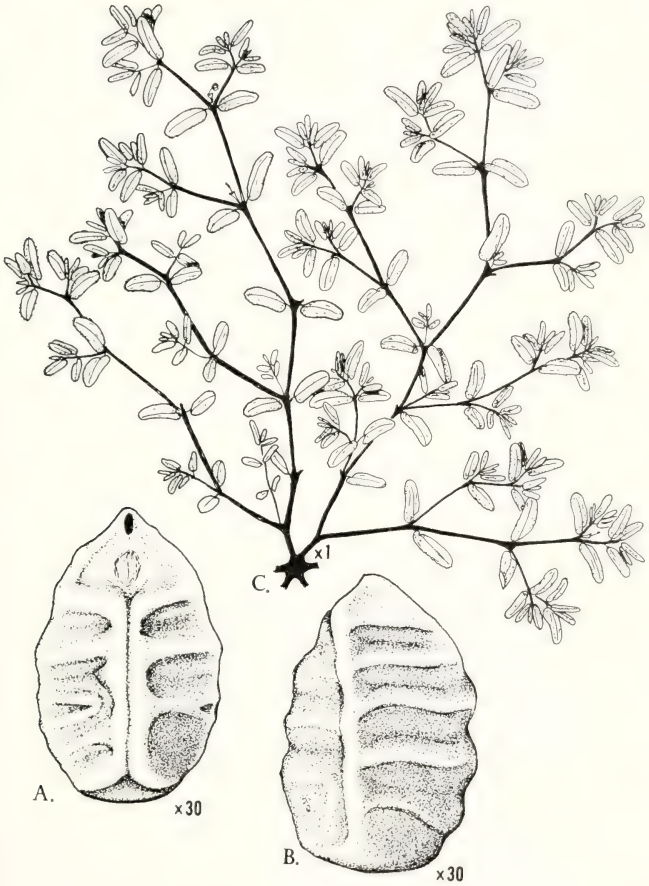
Annual; stems mostly prostrate, sometimes ascending or erect, 1.5-33.0 cm long, glabrous; internodes 0.5-77.0 mm long, typically ca. 20 mm; leaves glabrous, narrowly oblong, subfalcate to ovate, 3-13 mm long, 1-5 mm wide, apex obtuse to retuse, base unequal, larger side with lobe to 1.4 mm long, margin entire to serrulate with larger side serrulate to base, serrations on lobe prominent, margin on smaller side obscurely serrulate for less than ⅓ leaf length; petiole up to 1 mm long; stipules glabrous, to 1.5 mm long, fused basally, dissected above into 2 or more filiform segments; cyathia with peduncles 0.5-1.5 mm long, glabrous; involucre obconical, 0.5-1.0 mm long, glabrous outside, slightly pubescent on margins of lobes inside; lobes linear-lanceolate, glabrous except along margin, equalling or slightly exceeding glands in length; glands oblong to elliptic, less than 0.2 mm long, reddish in color; appendages white, wider than gland, margin entire to shallowly lobed; bracteoles reduced to 1, linear, apex entire or divided into 2-3 filiform segments at the apex; staminate flowers 1-2 (rarely none) per fascicle, 2-7 per involucre; gynophore erect to strongly reflexed at maturity; ovary glabrous; styles 0.4 mm long, bifid for ca. ⅓ length, clavate; mature capsules 1.2-1.8 mm long, 1.3-2.0 mm wide, glabrous, seeds 0.7-1.2 mm long, ca. 1.0 mm wide, ovate, angles sharp, ventral facets concave, transversed by 3-5 prominent ridges, dorsal facets convex, transversed by 5-7 prominent ridges, ridges passing more or less through angles, coat white to tan. Fig. 8.

HABITAT: In general, this species occupies areas of sandy and loamy soils of prairies, valleys, flood plains, roadsides, and waste areas.

RANGE: This is probably the most common species in our area and occurs over the entire four-state region and in almost every type of habitat available, from cracks in sidewalks to native prairie. Map 4.

Both varieties listed in synonomy can be identified from our area. However, as stated by Wheeler (1941), in var. *tenerrima* the small leaves exhibited

Fig. 8



Euphorbia glyptosperma Engelm.

FIG. 8. *Euphorbia glyptosperma*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

by this plant show no geographical correlation and completely intergrade with the more typical form. It probably represents more ecological or environmental rather than genetical variation. Var. *integrata* is very similar but differs in having entire leaves. However, the intergradation with the serrate leaves is complete and does not warrant separation.

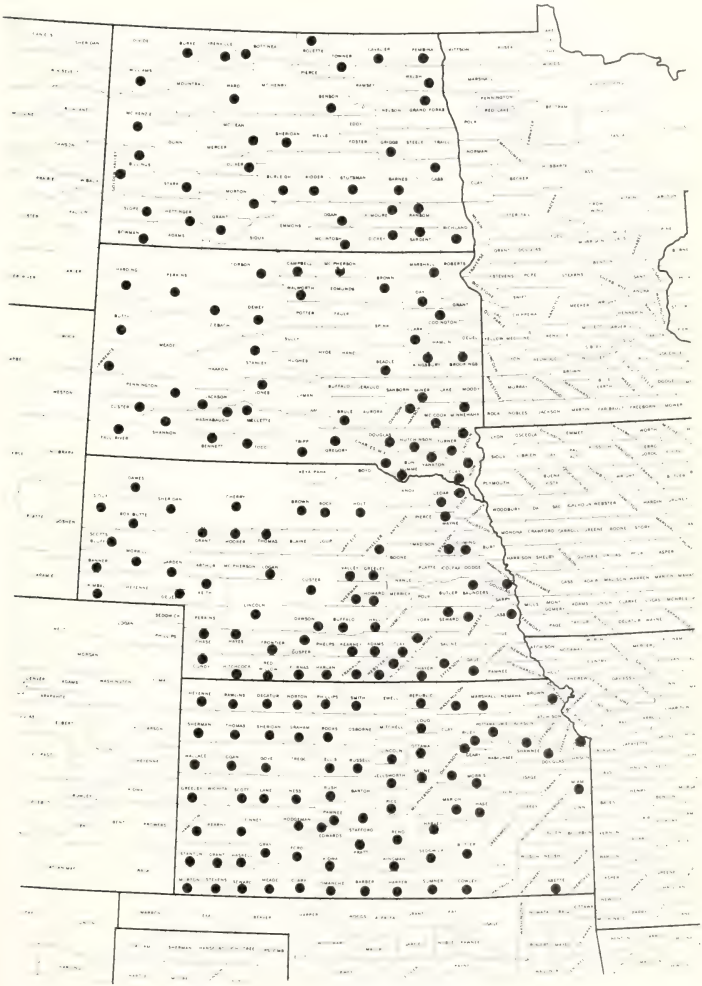
A rather interesting variation which more-or-less incorporates both of the varieties mentioned above occurs and appears to be directly correlated with available moisture and soil type. Many of the specimens collected (both personal and herbarium) from August and September exhibit a very distinct growth habit depending upon collection area. Material from hard, dry soils, such as immediately adjacent to roads and highways or from clay soils, have the younger portions of the stems with extremely reduced internodes and leaves which give a very dense crowded appearance; the leaves are usually reddish in color. This crowded condition will occur either over the entire plant or just at the tips of the branches on an otherwise rather typical-appearing plant. Again this appears to be a response to a possible reduction in available water since plants found in ditches or moist soil only a few feet away will be of the more typical form.

A specimen in the herbarium at KANU (*Richardson* 2321) from Turner Co., South Dakota, exhibited capsules that were characteristically three-celled while in addition many capsules had four cells and one capsule had as many as seven cells. Many of the capsules that were mature and of more than three cells appeared to have normal seeds except for being slightly compressed laterally; usually there were as many seeds as cells in the capsule. A seed from a capsule with six cells, however, indicated that two seeds had fused together as two raphes were visible. The only other abnormal feature observed in the plant was an extremely enlarged root which was found to be infected with mycelium of a fungus (unidentified). No correlation between the two is attempted, but further investigation is needed to determine whether there is any relationship between the fungus and the abnormal capsules. In addition, if further investigations do indicate a definite relationship, it remains to be seen why only the capsule if affected and not other parts of the plant.

7. **Euphorbia serpyllifolia** Pers., Syn. Pl. 2: 14. 1806. Type: "Hab. in Amer. Colidiore" s.n. (fragment MO!)

Annual; stems prostrate to erect, 5-30 cm. long, glabrous; internodes to 3.5 cm; leaves glabrous, spatulate, obovate or narrowly oblong to falcate, typically red mottled above along midrib, 4-15 mm long, 1-8 mm wide, apex obtuse, base unequal with larger side with lobe 0.1-1.0 mm long, margin serrate with serrations primarily at tip and along margins for less than ½ entire length from apex, petiole to 2 mm long; stipules free, glabrous, to 2 mm long, entire to dissected at apex into long attenuate, linear or linear-lanceolate segments; cyathia with peduncles 0.5-1.0 mm long, glabrous; involucre ob-

Map 4



conical to campanulate, 0.8-1.2 mm long, glabrous outside, pubescent inside at summit; lobes lanceolate, exceeding glands in length; with acute to acuminate apex, glabrous except slightly pubescent along inner margin, glands transversely oblong, 0.2-0.5 mm long, reddish in color; appendages white, wider than gland, entire to slightly lobed; bracteoles forming a rather broad portion between fascicles of staminate flowers, apex entire or dissected into 2-3 segments, glabrous to slightly pubescent at apex; staminate flowers 1-3 per fascicle, 5-12 per involucre; gynophore long and strongly reflexed at maturity; ovary glabrous; styles 0.2-0.7 mm long, bifid for less than ½ entire length, slightly inflated basally; mature capsules 1.5-2.1 mm long, 1.7-2.2 mm wide, glabrous, very sharply angled seeds 1.0-1.6 mm long, 0.6-0.8 mm wide, ovate to oblong, ventral facet concave, dorsal facets slightly convex with prominent ridge or keel between facets, facets smooth to very shallowly pitted-punctate or rugulose, coat white to light tan or brown. Fig. 9.

HABITAT: Areas of sandy or alluvial soils, in areas of disturbance. From personal collections, the species is the most abundant along roadsides and waste areas, rarely being found in native undisturbed situations.

RANGE: In the four-state region this species is relatively abundant in the Dakotas, particularly east of the Missouri River. It becomes progressively more scattered to rare in Nebraska. No specimens have been seen from Kansas. Map 5.

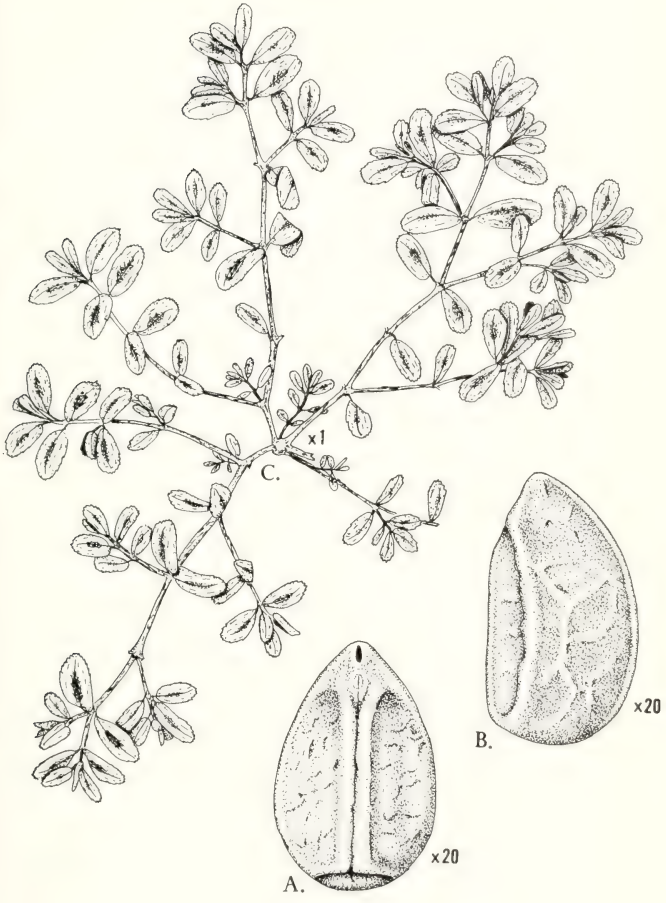
South central Nebraska appears to be the southern limit of the species. Wheeler (1941), however, lists it from Otero County in Southwestern Colorado and as far south as Texas and Mexico. Harrington (1964) also lists the species as scattered over Colorado. Consequently, the species would be expected from the western portion of Kansas and, in fact, both Rydberg (1932) and Gates (1940) list *E. serpyllifolia* Pers. (*albicaulis* of Rydberg) from Kansas. However, nearly all the *E. serpyllifolia* specimens I have examined were determined as *E. glyposperma* Engelm. or other species.

E. serpyllifolia and *E. glyptosperma* commonly occur together in the northern part of the area, except where rather arid conditions exist. Since the species are rather similar in general appearance, they are commonly misidentified. However, *E. serpyllifolia* Pers. tends to have smooth to rugulose seeds, red mottled spatulate to obovate leaves with serrations prominent in upper half of leaf and a rather robust decumbent to ascending habit. *E. glyptosperma* Engelm. has definitely transversely ridged seeds, uniformly green oblong to subfalcate leaves with serrations extending to base on lobed side and typically a prostrate slender habit.

8. **Euphorbia lata** Engelm. in Emory, U.S. & Mex. Bound. Surv. 2 (1): 188. 1859. Type: "Pope's Expedition" s.n. (NY; isotype G; photographs F).

Perennial; stems decumbent to ascending, 7-15 cm long, uniformly pubescent with short appressed hairs; internodes to 2 cm long; leaves uniformly

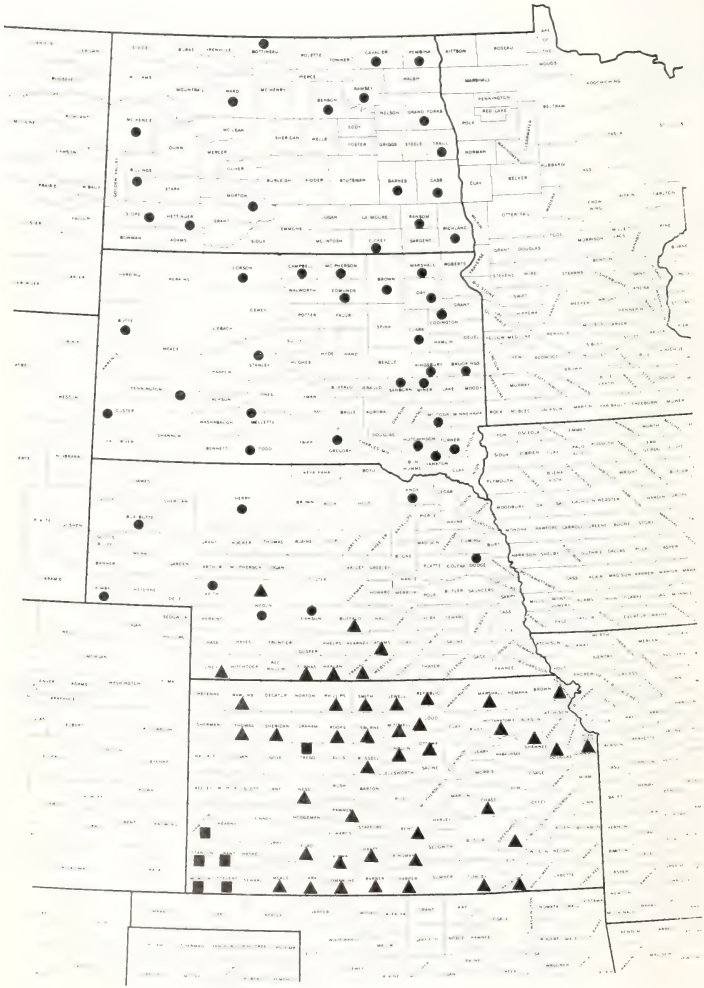
Fig. 9



Euphorbia serpyllifolia Pers.

FIG. 9. *Euphorbia serpyllifolia*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

Map 5



puberulent, ovate to broadly falcate or long-deltoid, margin typically revolute giving linear appearance, 3-10 mm long, 1-5 mm broad, apex obtuse, base truncate to slightly cordate, margin entire; petiole to 1 mm long; stipules free, to 5 mm long, linear-lanceolate, pubescent along margin with long slender hairs; cyathia with peduncles less than 3 mm long, puberulent; involucre turbinate, 1.7-2.0 mm long, puberulent outside primarily on longitudinal low ridges running from the base to lobes, glabrous inside except at summit; lobes deltoid, pubescent along margin, equalling or very slightly exceeding glands in length; glands transversely oblong; 0.5-1.2 mm long, stipes on the inside bearing many long slender hairs which slightly extend over the inner lip of gland; appendages white, reduced, less than 0.5 mm long, narrower or only equaling the gland in width, margin entire to crenate; bracteoles adnate only at base with involucre, dissected above with many slender segments, pubescent at apex and along margin; staminate flowers 5-7 per fascicle, 25-35 per involucre; gynophore puberulent, shortly exerted, slightly reflexed; ovary uniformly puberulent; styles 1 mm or less long, bifid for ½ entire length, clavate; mature capsules 2.0-2.5 mm long, 2.3-2.7 mm wide, puberulent, usually only 1 or 2 (rarely all 3) seeds maturing; seeds 1.7-2.0 mm long, ca. 1.0 mm wide, long-deltoid to long ovate, angles sharp, ventral facets concave and smooth, dorsal facets convex, smooth to slightly rugose, coat white. Fig. 10.

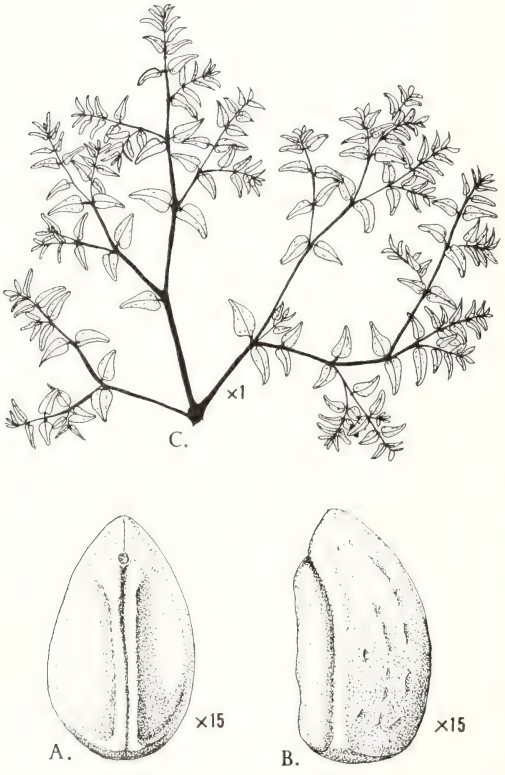
Habitat: Short grass loam to dry, rocky, sandy prairies. Information from herbarium sheets indicate the species is rather common on south and west facing bluffs.

Range: Collections from only the southwest portions of Kansas with one collection from west central Kansas (Trego Co.). Map 5.

9. **Euphorbia prostrata** Ait., Hort, Kew. 2: 139. 1789. Type: "Native of the West Indies. Cult. 1758, by Mr. Philip Miller" (British Museum if extant).
Euphorbia chamaesyce Wheel. Rhodora 43: 265. 1941.
Chamaesyce malaca Small, Fl. Se. U.S., 713, 1333. 1903. Type: Kerrville, Kerr Co., Texas, June 26-30, 1894, *Heller 1918*. (NY; isotypes F, G, MO!).

Annual; stems prostrate to erect, 4-40 cm long, short crisp hairy above, glabrate to sparingly pubescent below; internodes mostly 1-2 cm long on main stem; leaves uniformly crisply hairy below, upper glabrous to sparingly pubescent mainly near apex, broadly elliptical, oblong, obovate-spatulate to ovate, 3-15 mm long, 2-8 mm wide, apex broadly rounded to obtuse, base unequal with larger side with lobe less than 1.0 mm long, margin minutely serrate, predominantly near apex; petiole up to 1.0 mm long, stipules with short pubescence along margin, 0.3-1.0 mm long, dorsal stipules usually free with ventral stipules usually united basally, triangular to laciniate; cyathia with puberulent peduncles 1-2 mm long; involucres obconical, 0.5-1.0 mm long, puberulent outside, glabrous inside except at summit; lobes narrowly ovate

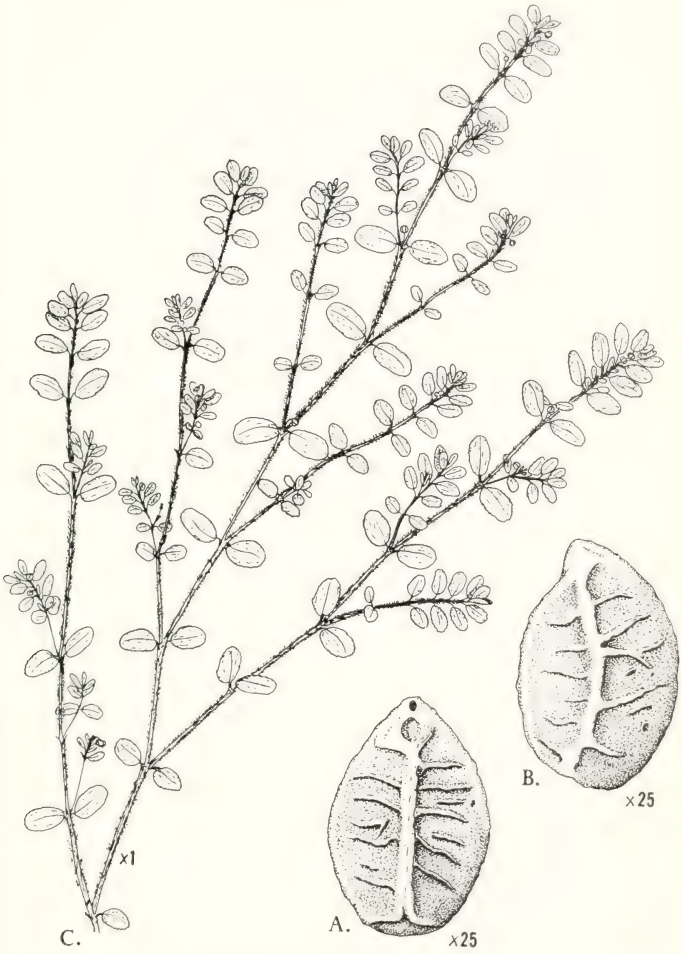
Fig. 10



Euphorbia lata Engelm.

FIG. 10. *Euphorbia lata*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

Fig. 11



Euphorbia prostrata Ait.

FIG. 11. *Euphorbia prostrata*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

to triangular, exceeding glands in length, bearing short stiff hairs along margin; glands oval to transversely oblong, reddish in color; appendages minute, reddish to white in color not exceeding gland in width or length, margin entire; bracteoles reduced to 2 or 3, glabrous filiform segments, pubescent along margin; staminate flowers 3-6 per involucre; gynophore hairy above, glabrate below, exerted and reflexed at maturity; ovary densely white-hairy; styles 0.2-0.3 mm long, bifid nearly to base, clavate; mature capsule 1.2-1.5 mm long, 1.4-1.8 mm wide, prominently pilose-villous below equator with pubescence extending to apex only along angles of capsule; seeds 0.9-1.1 mm long, 0.5-0.7 mm wide, ovate, angles sharp, facets traversed by low, narrow, sharp, granular, irregular ridges, scarcely passing through angles, ventral facets slightly concave, dorsal plane to slightly convex, coat white to brown. Fig. 11.

HABITAT: Frequently in dry to moist sandy loam from prairie pastures and waste areas to roadsides, ditches and embankments.

RANGE: Southcentral and northern one-half of Kansas to southcentral Nebraska. Map 5.

Wheeler (1941) treated *E. prostrata* Ait. as a synonym of *E. chamaesyce* L. based on a specimen from a collection of P. Browne from Jamaica. As indicated by both Croizat (1945) and Burch (1966), the collections of Browne were not seen by Linnaeus until 1758, when he purchased Browne's collections (Stearn, 1957).

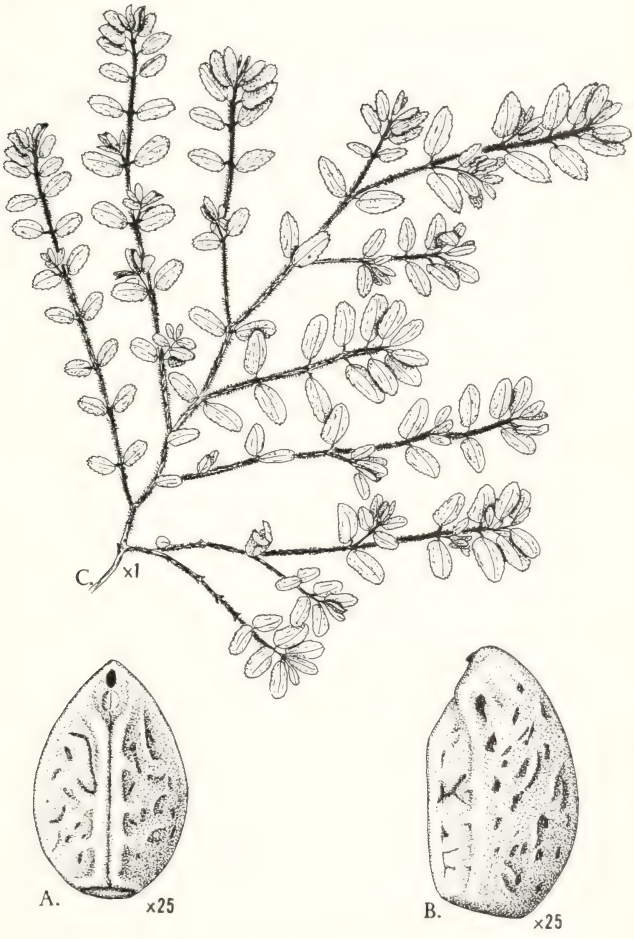
Croizat (1945) gives a rather complete discussion of the problems injected by Wheeler and maintains that the two taxa are distinct with *E. prostrata* Ait. as the correct name to be applied to the plant of our area. As Burch (1966) states, Wheeler accepted the usage of *prostrata* later and used it in a supplement to the second edition of Kearney & Peebles *Arizona Flora* published in 1962; but this has been overlooked by most authors.

In general, this species should not be confused with any of our area because of the sharply, transversely-ridged seeds and the capsules which are conspicuously pubescent on the angles, particularly below the equator.

10. **Euphorbia stictospora** Engelm. *in* Emory, U.S. & Mex. Bound. Surv. 2 (1): 187. 1859. Type: Steep bank of the Pawnee River ("Fork"), in loose soil, Kansas, Sept. 8, 1847, *A. Fendler* 798 (MO!).

Annual; stems prostrate to ascending, 5-45 cm long, crisply villous throughout, with hairs multicellular and 0.7-1.0 mm long, internodes on main stem 1-2 cm long, progressively shorter on lateral branches; leaves sparsely long crisply hairy and glabrate above, densely long crisply villous beneath, ovate, suborbicular to oblong-linear, 3-15 mm long, 2.5-10.5 mm wide, apex acute to broadly obtuse or rounded, base unequal with larger side with lobe 0.1-1.2 mm long, margin serrate to serrulate at apex, teeth extending $\frac{3}{4}$ of leaf length from apex on lobed side, to only about $\frac{1}{3}$ leaf length on smaller side; petiole 1-2 mm long, densely villous; stipules sparsely pilose

Fig. 12



Euphorbia stictospora Engelm.

FIG. 12. *Euphorbia humistrata*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

to villous, 1.0-1.5 mm long, dorsally distinct to variously united ventrally, triangular, often attenuate; cyathia with peduncles 1-2 mm long, puberulent solitary at nodes, but very congested on short leafy lateral branches; involucre obconical, 0.7-1.0 mm long, pubescent outside, glabrous inside except along margins of lobes; lobes triangular to linear-lanceolate, glabrous except for margins, equaling glands in length; glands subcircular to transversely oblong, less than 1.0 mm long, reddish; appendages white, minute to slightly longer than width of gland, entire to sharply toothed; bracteoles minute, linear; staminate flowers 1-3 per fascicle, 3-9 per involucre; gynophore glabrous below, villous above, exerted and reflexed at maturity; ovary densely strigose; styles ca. 0.2-0.5 mm long, entire to deeply emarginate, clavate, mature capsule 1.4-2.3 mm long, 1.2-2.0 mm wide, strigose to hirsute; seeds 1.0-1.5 mm long, 0.5-0.7 mm wide, narrowly ovate to oblong-ovate, sharply angled, base truncate and concave, facets with shallow irregular pits or irregular low ridges and furrows, coat typically tan to white with brown mottling due to testa showing through at bottom of pits or furrows. Fig. 12.

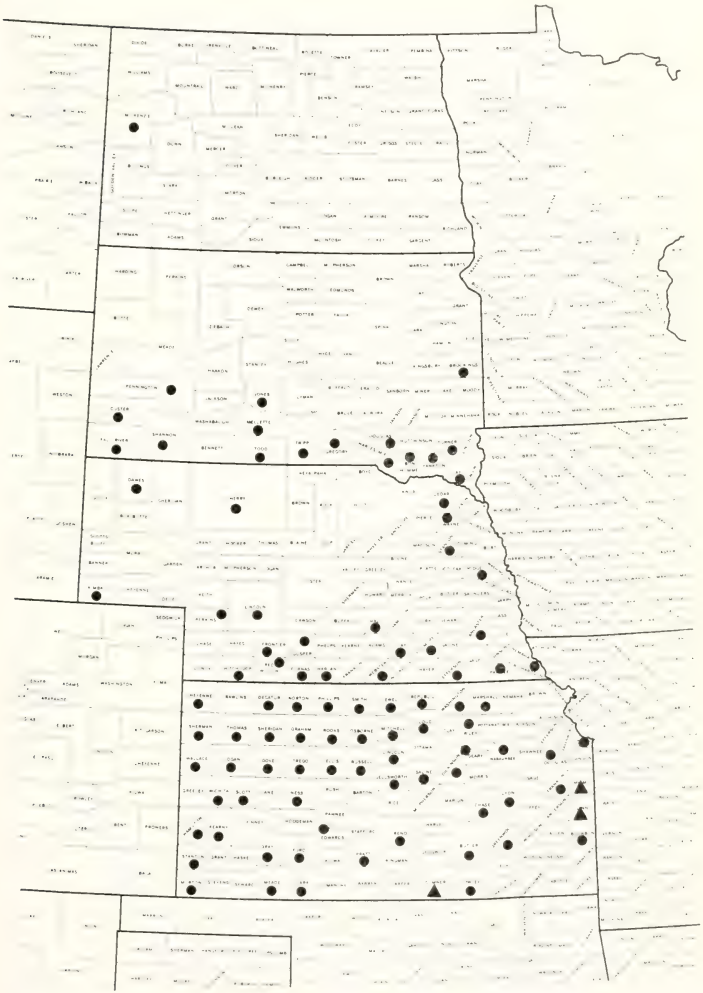
HABITAT: Dry, moist, sandy soils along roadsides, waste areas and cultivated fields. This species also appears to be one of the few of this subgenus which is common in native prairies, particularly western parts where it occurs in the rather open areas between clumps of short grasses.

RANGE: Records over Kansas and Nebraska except for scattered collections over southeastern one-half of Kansas and the sandhills portion of northcentral Nebraska. The northern extention of the range appears to be the southern one-half of South Dakota with one record (McKenzie Co.) from as far north as westcentral North Dakota. Map 6.

E. stictospora Engelm. is often confused with *E. humistrata* and *E. maculata*. In general, *E. stictospora* Engelm. can be distinguished from the others by the long, dense, crisply villous to strigose pubescence on the stems, lower leaf surfaces and ovary. The seeds are irregularly pitted or wrinkled, with the base truncate and prominently concave. The seeds usually have a thin coat at the bottom of the pits or furrows with the dark brown testa showing through, giving the seed a punctate appearance.

A specimen in the herbarium at KANU *(Richardson & Robertson 1388)* from Kimball Co., Nebraska, possess an interesting abnormal development of several lateral branches and the subsequent involucreas: several nodes indicated the development of a lateral branch. However, the branch apparently did not separate properly and remained fused with the main axis to form a broad, flattened stem which continued, in most cases, to the apex. In a few cases the branch did separate, not at the node, however, but somewhere along the internode region. A cross-section of this internode region revealed as many as four complete steles fused together. At many of the nodes, three or rarely four leaves were present. Many of the cyathia that were produced on

Map 6



these abnormal lateral branches were also abnormal. First, there were usually two or more cyathia per node instead of the usual one; and at many nodes complete fusion between cyathia had occurred. From one broad flat peduncle as many as four developing ovaries were counted with the equivalent number of subsequent other parts visible. For example, four complete sets of glands and appendages and staminate flower fascicles were noted. The seeds from these capsules appeared normal, but no germination was attempted to test viability. This aberration was apparently restricted to an individual plant since other plants taken in the immediate vicinity did not show any abnormal development.

11. **Euphorbia humistrata** Engelm. ex Gray, Man. Bot. No. U.S., ed. 2, 386. 1856. Type: Banks of the Mississippi, St. Louis, Missouri. July, 1833, *Engelmann 1139* (MO!).

Annual; stems prostrate to ascending, to 35 cm long, puberulent to tomentose or pilose, particularly along sides of stem and younger portions of stem, typically glabrate below; internodes 1-3 cm long; leaves glabrous to very sparsely pilose, orbicular, oval, to oblong-ovate on main stems, typically red mottled above, 5-15 mm long, 3.5-11.0 mm wide, apex broadly rounded to obtuse or emarginate, base strongly unequal with larger side with lobe 0.5-2.5 mm long, margin entire to remotely serrulate, with lateral branches bearing often more narrow and reduced leaves; petiole 1.0-1.5 mm long, glabrous to villous only on dorsal side; stipules glabrous to slightly pubescent along margin; 1.0-1.5 mm long, typically united (rarely free) into a large membranaceous scale dissected into linear to filiform segments at apex, cyathia solitary at nodes, but usually congested on the short leafy lateral branches, peduncles ca. 1.0 mm long, crisply hairy to glabrate; involucre obconical, 0.6-2.0 mm long, tapering to peduncle, sparingly villous outside, glabrous inside; lobes triangular, attenuate, glabrous, slightly exceeding glands in length; glands transversely oblong to elliptical, 0.1-0.5 mm long, reddish; appendages white to red, 1-2 times longer than width of gland, entire to crenulate; bracteoles minute, linear; staminate flowers 3-8 per involucre; gynophore slightly vestite above, barely exerted and reflexed at maturity; ovary densely strigose; styles 0.6-0.9 long, bifid for ½ entire length, slender; mature capsules 1.0-1.5 mm long, 1.2-1.7 mm wide, strigose to glabrate; seeds 0.9-1.0 mm long, 0.6-0.8 mm wide, broadly ovate to oblong, angles low and rounded to shape, facets granular smooth to tuberculate or with low irregular transverse ridges, ventral facets slightly concave, dorsal plane to slightly convex, coat white to reddish brown. Fig. 13.

HABITAT: From the limited information available, this species is found in areas of rather moist loam to sandy lowland areas. Most commonly encountered on mud flats (usually surface dried) or sandy soils along rivers or lakes.

RANGE: This species has been reported from only three counties in eastern

Fig. 13

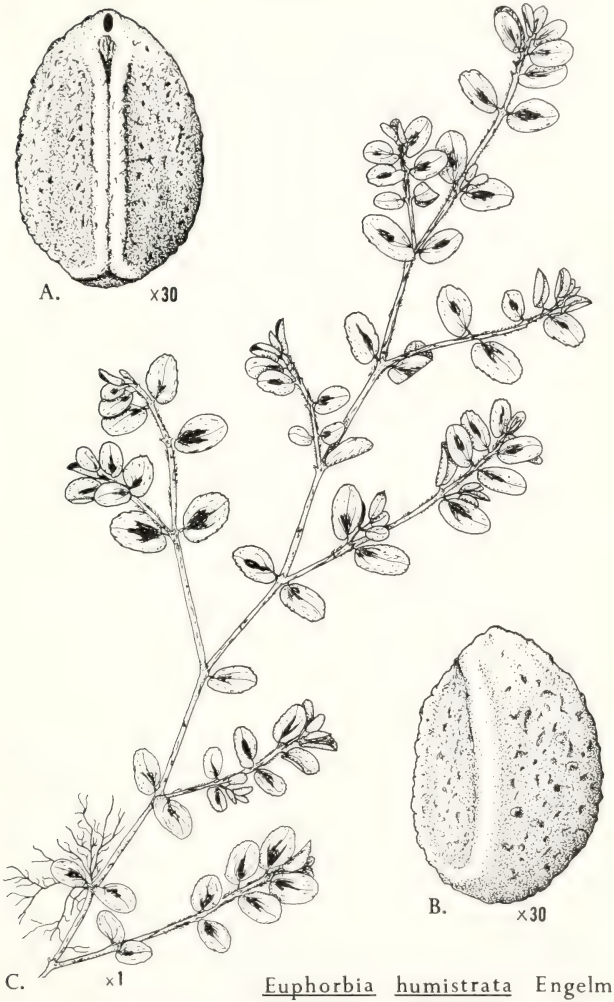


FIG. 13. *Euphorbia stictospora*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

and southcentral Kansas. Most authors, however, list this species as extending over the eastern one-third of the state. From personal collections, where the species does occur (Linn Co.), the plants are rarely encountered and relatively restricted in habitat. With additional collections, it may be found to extend well into the state as would be indicated by the collection from Sumner Co., Kansas. Map 6.

E. humistrata approaches very closely the broad-leaved forms of *E. maculata* and is often confused with it in areas where both species occur. In order to help eliminate some of the confusion, the following chart is provided in an attempt to give some of the major distinctions which I have found to be useful in the separation of the two species.

E. humistrata Engelm.	*E. macultata* L.
Stems:	Stems:
puberulent to tomentose or pilose	densely hispid to sericeous
young portions glabrate below with sides of stem densely pubescent giving winged appearance	uniformly pubescent throughout
hairs ca. 0.2-0.5 mm long	hairs ca. 0.5-1.0 mm long
Leaves:	Leaves:
orbicular, oval to oblong-ovate	elliptic-ovate, oblong-ovate to linear-oblong or subfalcate
glabrous to sparsely pilose below	usually velutinous to villous below
3.5-11.0 mm wide	2-6 mm wide
apex broadly rounded to obtuse or emarginate	apex acute to obtuse
margin entire to remotely serrulate	margin serrate to base on lobed side, to ½ length on smaller side
Stipules:	Stipules:
united into large white membranaceous scale on younger portions of stem	distinct, small
dissected above into short linear to filiform or lanceolate segments	dissected for ½ length or more into linear-lanceolate segments
Styles:	Styles:
0.5-0.9 mm long	0.1-0.5 mm long
bifid for ½ length	bifid for ⅓ length
slender	clavate
Seeds:	Seeds:
coat granular	coat smooth
facets smooth to tuberculate or with low irregular ridges not passing through angles of seed	facets traversed by 3-5 low ridges which generally pass through angles of seed
angles low rounded	angles sharp

12. **Euphorbia maculata** L., Sp. Pl. 1: 455. 1753.
E. supina Raf., Amer. Monthly Mag. 2: 119. 1817.

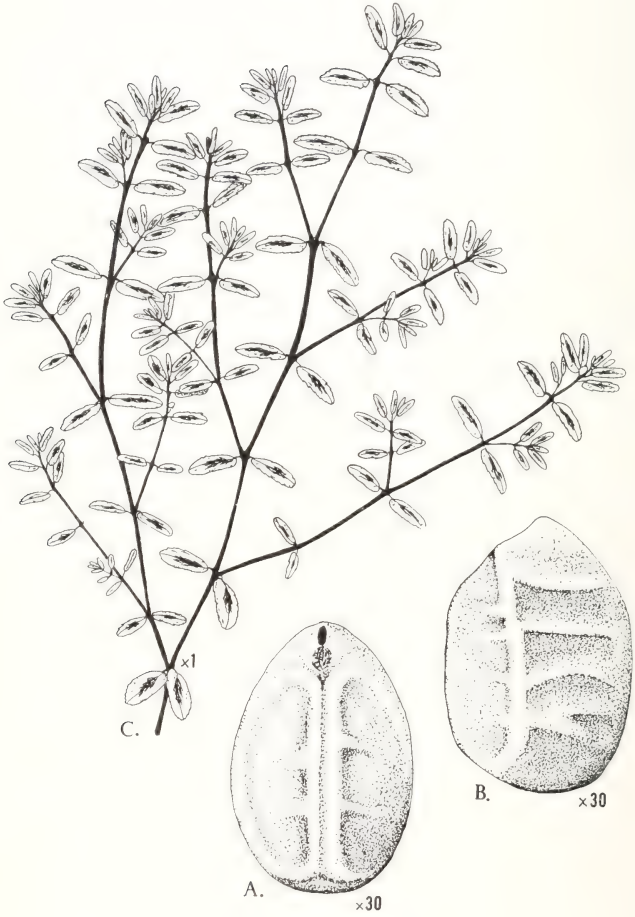
Annual; stems prostrate to ascending, 5-45 cm long, sparsely villous or densely hispid to sericeous; internodes 10-15 mm on main stem; leaves velutinous to villous below; glabrate above, elliptic-ovate, oblong-ovate to linear-oblong or subfalcate, typically red mottled above along midvein, green to reddish below, 4-17 mm long, 2-6 mm wide, apex acute to obtuse, base unequal, larger side with lobe 0.1-1.2 mm long, margin serrate on larger side to base of lobe, to only about ½ leaf length on smaller side, leaves of lateral branches tending to be more oblong, petioles 1.0-1.5 mm long, glabrous above, villous on sides and below; stipules pubescent along margins, 1.0-1.5 mm long, distinct, dissected above into 2-3 linear-lanceolate to filiform segments; cyathia solitary at nodes usually on short congested leafy lateral branches; peduncles long, glabrous to sparsely pubescent; involucres obconical, less than 1.0 mm long, sparingly villous outside, essentially glabrous inside; lobes triangular to linear-lanceolate, glabrous except margins with few long hairs, equaling or exceeding glands in length; glands transversely elongate, less than 0.5 mm long, red; appendages white to red, minute, 0.1-0.6 mm long, entire to crenulate; bracteoles reduced, linear-lanceolate with apex dissected into filiform segments, pubescent along margin; staminate flowers 2-5 per involucre; gynophore exerted and strongly reflexed; ovary densely strigose; styles 0.1-0.5 mm long, bifid for ⅓ length, clavate; mature capsules uniformly pubescent with short appressed stout hairs; seeds 0.8-1.2 mm long, 0.5-0.7 mm wide, oblong to ovate, sharply angles, facets traversed by 3-5 rather regular low ridges, often passing through the angles, ventral facets concave, dorsal plans to slightly convex, coat white to brown, rarely slightly granular. Fig. 14.

Habitat: Most common along roadsides, waste areas of places of disturbance such as old cultivated fields which have been allowed to grow back with weeds. This species also will enter prairies by invading around the margin or along fence rows.

Range: Eastern two-thirds of Kansas; south and eastern portions of Nebraska, with scattered collections from the western one-half of the state; southeastern South Dakota with one collection from the Black Hills region (Pennington Co.); east central (Cass Co.) and south central (Morton Co.) North Dakota. Map 7.

According to Burch (1966), controversy as to the name to be applied to this plant arises from an entry on a herbarium sheet in the Linnaean Herbarium. The number appearing on the sheet is different from what appears in *Species Plantarium*. The number refers to an erect form (similar to the one on the sheet) while the name refers to a prostrate plant in *Species Plantarum*. Wheeler (1960) decided the name was correct and applied *E. maculata* to the erect form (*E. nutans* of this paper).

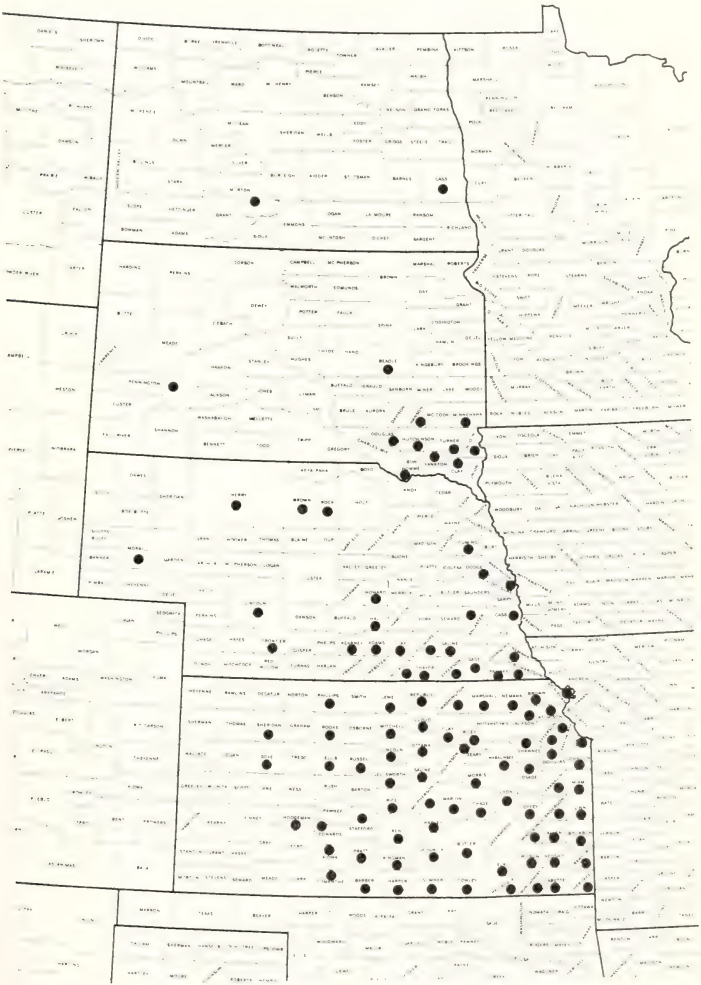
Fig. 14



Euphorbia maculata L.

FIG. 14. *Euphorbia maculata*. A. Raphial view of seed. B. Side view of seed with raphe on the left. C. Habit of plant.

Map 7



Croizat (1962), however, has shown that Linnaeus methodically set up the arrangement of the species of *Euphorbia* by placing the succulent forms first, followed by the shrubby types, with the next series being a group with erect habit and serrate leaves, and the last group being prostrate. The application of the name *maculata* to the prostrate form as indicated by *Species Plantarum* seems to be the correct one to follow.

Burch (1966) added further evidence from the examination of books in the Linnaean Library which indicated Linnaeus knew "maculata" as a prostrate plant.

13. **Euphorbia hexagona** Nutt.; Spreng., Syst. 3: 791. 1826.

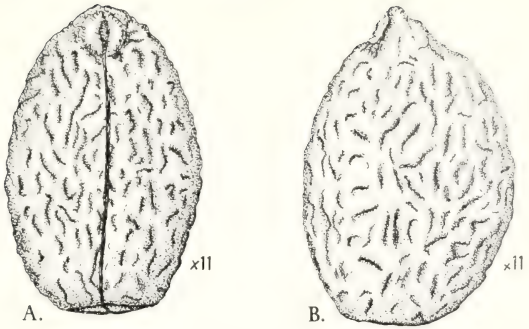
Annual; erect, 20-50 cm tall, sparingly hairy, yellowish-green in color, branches very slender, ascending to erect; leaves opposite, glabrous to appressed hirsute, particularly on lower surface of young leaves, cauline leaves broadly linear to oblong or lanceolate to narrowly elliptic, 1-7 cm long, 1-15 mm wide, apex acute, margin entire, base tapering equally to petiole, leaves of lateral branches linear-lanceolate to filiform; petioles ca. 1.0 cm long, hirsute; stipules minute or absent; peduncles up to 2 mm long, hirsute; involucre campanulate, 1.5-3.0 mm long, appressed hirsute outside, glabrous to pubescent with long slender hairs beneath gland; lobes triangular, glabrous inside, hirsute outside, fimbriate and folded over mouth of involucre, equaling to slightly exceeding glands; glands transversely oblong-ovate to subcircular, greenish-yellow, sessile to subsessile; appendages greenish-yellow to white, 2-3 times longer than width of gland, triangular-ovate, entire usually erect; bracteoles partially enclosing staminate flowers, fused for less than ½ total length dissected above into many linear segments, not extending from involucre, each bearing many marginal hairs; staminate flowers 4-10 per fascicle, 20-40 per involucre; gynophore glabrous, long exerted, up to 5 mm beyond involucre, erect to strongly reflexed; styles to 1.0 mm long, bifid for ½ length, clavate; mature capsule 3-5 mm long, to 4 mm wide, glabrous; seeds 2.5-3.3 mm long, 1.7-2.6 mm wide, ovoid to oblong, globose in cross section, papillose, tuberculate or roughened, coat white, brown, or black, tops of tubercules or roughened surface usually lighter in color with area between dark. Fig. 15.

HABITAT: Dry sandy soils of roadsides, prairies and valleys.

RANGE: Western two-thirds and the central-northeastern portions of Kansas; scattered through all but southeastern one-fourth of Nebraska; scattered in southern South Dakota. Although the species is reported from the sand hills region of Nebraska, personal collections indicate this species is most commonly encountered at the margins of this and similar areas, and rarely in the loose sandy type soil typical of these areas. Map 8.

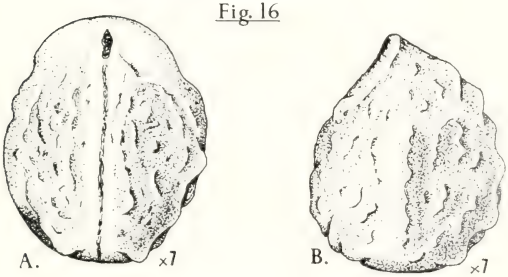
Both Engelmann (*in* Emory, 1859) and Fernald (1950) indicate that the

Fig. 15



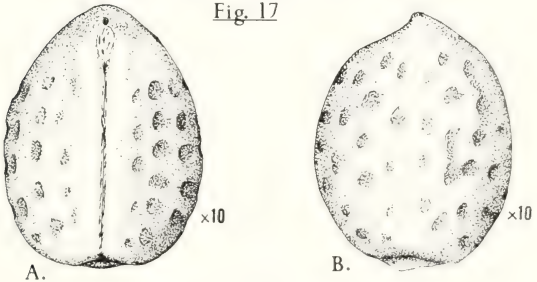
Euphorbia hexagona Nutt.

Fig. 16



Euphorbia marginata Pursh.

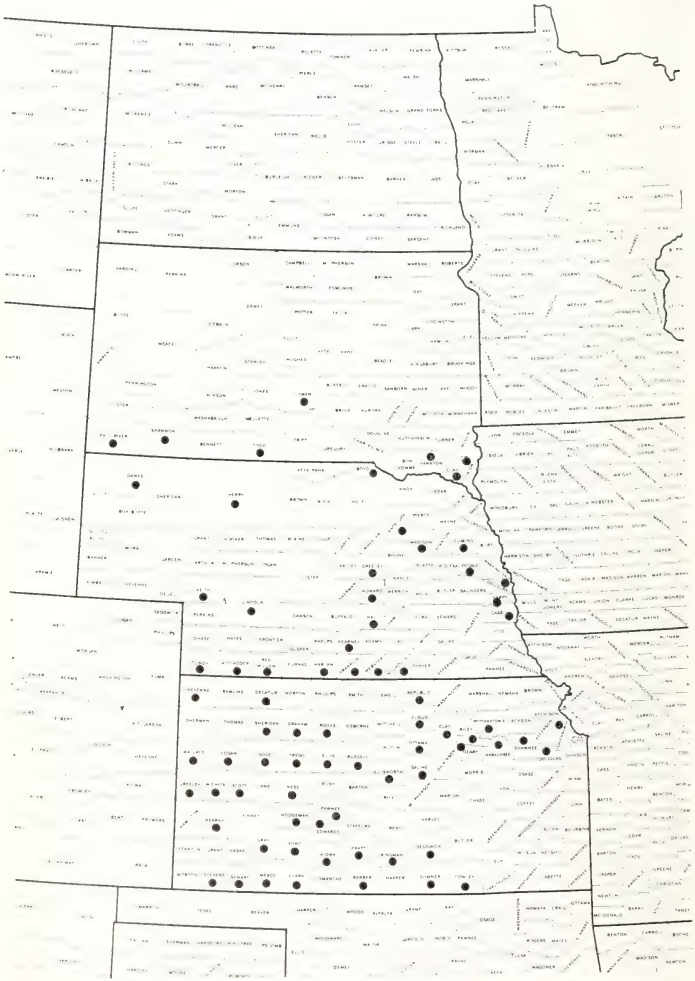
Fig. 17



Euphorbia corollata L.

Fig. 15. *Euphorbia hexagona* A. Raphial view of seed. B. Side view of seed with raphe on the left. Fig. 16. *Euphorbia marginata*. A. Raphial view of seed. B. Side view of seed with raphe on the left. Fig. 17. *Euphorbia corollata*. A. Raphial view of seed. B. Side view of seed with raphe on the left.

Map 8



branches of the main stem contain scattered cyathia, most of which are unisexual and contain only staminate flowers, with a few having pistillate flowers.

Examination of material from our area indicated just the reverse in that most of the cyathia of lateral branches contained both pistillate and staminate flowers and very rarely contained only staminate. In many cases, however, it was evident that the pistillate flower was reduced and undeveloped in many of the cyathia while in others the capsules were exerted and well developed. A high degree of variability exists from plant to plant. Many plants which were collected late in the season showed either dehisced or mature capsules and seed from virtually every cyathia. Other plants indicated very limited seed production from cyathia on lateral branches, while still other plants showed a mixture of both developed and aborted pistillate flowers on lateral branches.

14. **Euphorbia marginata** Pursh. Fl. Am. Sept. 2: 607. 1814.

Annual; erect, 30-90 cm tall, densely villous to pilose, usually unbranched below rays of terminal inflorescence; cauline leaves alternate, whorled at base of umbel, glabrous to pubescent basally or along midrib, broadly ovate to elliptic or obovate-oblong, 1.5-10.0 cm long, 0.5-6.0 cm wide, apex acute, margin entire, base equal, sessile; floral leaves and bracts whorled or opposite, conspicuous broad white to pink margin; stipules small and soon deciduous; inflorescence umbel-like, 3-4 (rarely 5) rayed with each ray again branched several times; glabrate to woolly particularly on younger portions of stem; peduncles up to 5 mm long on lateral branches, with peduncles as much as 3.5 cm long in axil of main branches of inflorescence; involucre campanulate, 3-4 mm long, villous to pilose outside, densely pubescent inside with short soft hairs; lobes broad, apex deeply fimbriate, segments glabrous, greatly surpassing glands, curved over mouth of involucre; glands transversely oblong, ovate or rounded, 1.0 mm wide, 1.0-1.8 mm long, light to dark green; appendages white, prominent, conspicuously wider and longer than gland, up to 2 mm long, reniform to broadly ovate; bracteoles forming radial partion between fascicles of staminate flowers, adnate basally, dissected above into many filiform segments, pubescent from base to ca. ¾ entire length, prominently exerted beyond summit of involucre; staminate flowers 12-25 per fascicle, 60⁻ per involucre; anthers puberulent to glabrous, prominently yellow-green in color; gynophore long exerted, sharply reflexed at maturity, hirsute to woolly to base; styles 1.0-2.5 mm long, bifid for ⅔ of length, short appressed hairs nearly to apex along outer surface of stigma; mature capsule 4-6 mm long, 5-7 mm wide, hirsute to woolly; seeds 3-4 mm long, 3.0-3.5 mm wide, ovoid-globose, prominently tuberculate, often reticulate-tuberculate, coat white to light tan. Fig. 16.

HABITAT: Mostly of dry sandy to rocky soils of disturbed prairie pastures, waste areas, roadsides or abandoned cultivated fields. Usually abundant along and in shallow ravines or dry eroded areas in heavily grazed prairie pastures; rarely found in native undisturbed prairies.

RANGE: A variable species common in Kansas and southern one-half of Nebraska and South Dakota with scattered collections from the northern one-half of Nebraska, northeastern South Dakota, east-central and west-central North Dakota. Stevens (1963) suggests that perhaps the plants in North Dakota have escaped from cultivation since it is often grown as an ornamental. The limited amount of information available on herbarium sheets and the fact that no other collections have been seen to indicate otherwise would tend to support this suggestion. Map 9.

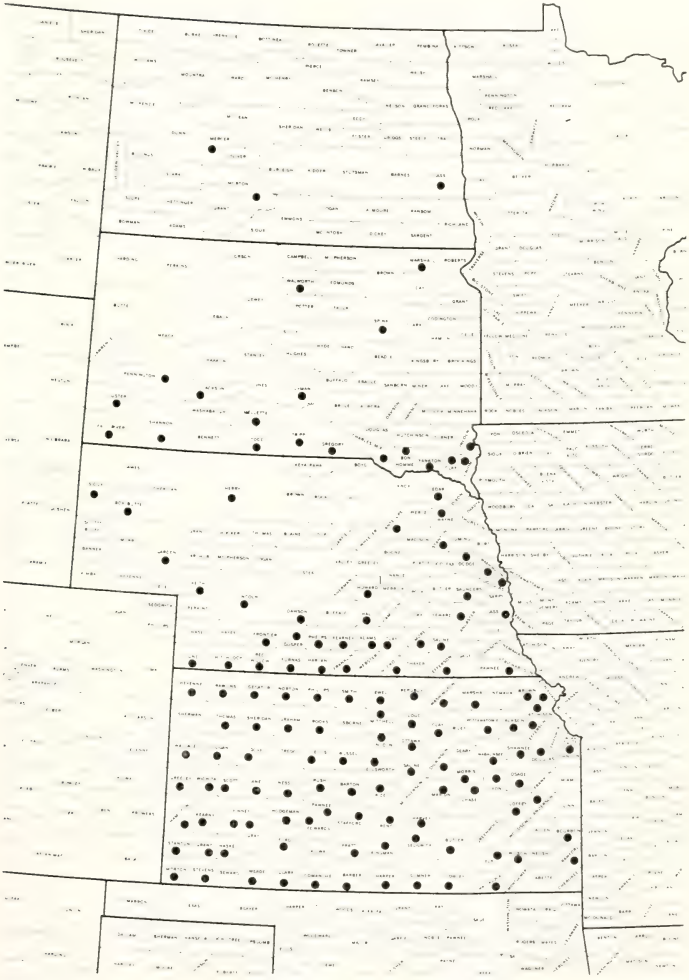
15. **Euphorbia corollata** L. Sp. Pl. 459. 1753.

Perennial; erect, to 1 m tal, glabrous to villous or pilose, rarely branching below inflorescence; cauline leaves alternate, whorled at base of umbel, glabrous to soft-pubescent, particularly below, oblong, lanceolate, elliptic or spatulate, 1-6 cm long, 0.5-1.7 cm wide, apex acute or obtuse to slightly emarginate, margin entire, base equal, sessile to short petiolate; floral and bracteal leaves opposite, oval to oblong or broadly lanceolate, 1.0-2.5 cm long, 0.5-1.0 cm wide, typically with small white margin extending from ca. ½ leaf length to apex; inflorescence umbellate, 3-7 rayed, rays dichotomously branched several times; peduncles 0.3-3.0 (4.5) cm long; involucres broadly campanulate, 1-2 mm high, essentially glabrous outside with scattered hairs at base of gland, densely pubescent inside beneath glands; lobes broad, entire to lancerate, surpassing glands, densely pubescent with short hairs; glands rounded to transversely oblong, greenish yellow; appendages white, 0.5-3.5 mm long, 0.2-2.2 mm wide, suborbicular to obovate or oblong to rhombic, rarely emarginate, glabrous, with a few short stiff hairs below at junction with gland; bracteoles forming large radial partition between fascicles of staminate flowers, tending to surround fascicles, entire to dissected at apex, densely pubescent, slightly emerging from involucre; staminate flowers 4-6 per fascicle, 20-30 per involucre; ovary with scattered short appressed hairs basally along sides of sutures, becoming glabrous as capsule matures; styles to 1.0 mm long, bifid for ½ entire length, spreading; capsules 3-4 mm long, 3.0-5.2 mm broad; seeds 2.2-3.0 mm long, 1.5-2.2 mm wide, subglobular to ovate, facets smooth or with large shallow depressions arranged in irregular longitudinal rows, coat white to gray, rarely punctate. Fig. 17.

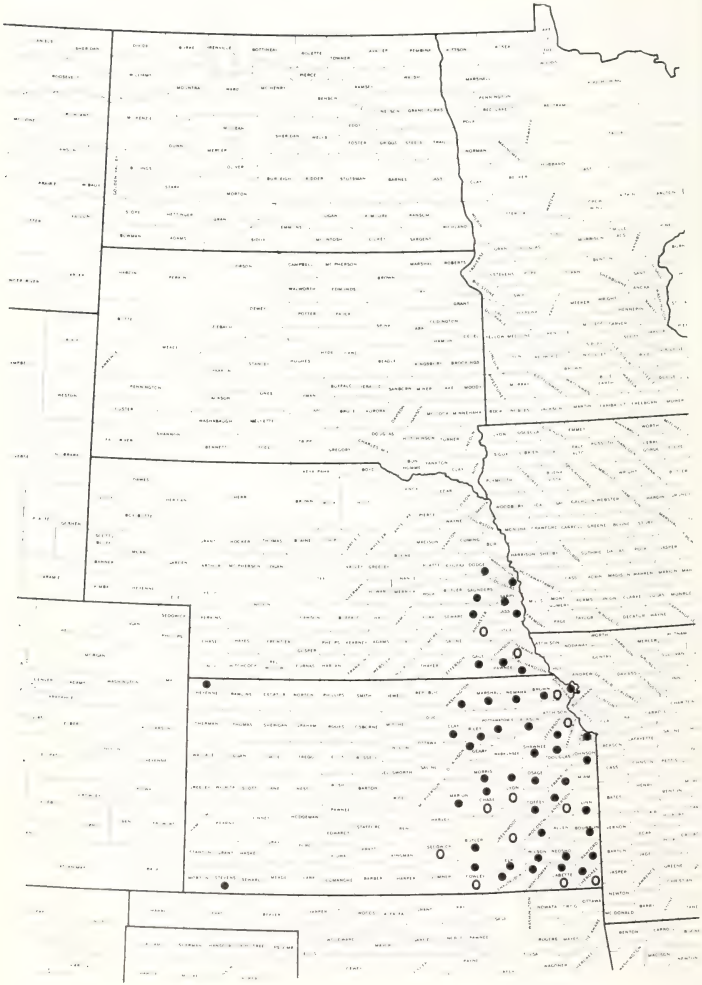
Two varieties are recognized and distinguished as follows:

a. Plants glabrous throughout ..... 15a. *E. corollata* var. *corollata*
a. Stems and/or leaves variously pubescent ..... 15b. *E. colorollata* var. *mollis*

Map 9



Map 10



15a. **Euphorbia corollata** L. var. **corollata.**

HABITAT: Dry to moist sandy or loam soil of open woodlands, clearings, roadsides, waste areas or prairies.

RANGE: Primarily southeastern portion of Nebraska and eastern third of Kansas, with two collections (Cheyenne Co. & Stevens Co.) from extreme western Kansas. Map 10.

E. corollata var. *corollata* is a quite variable variety in our area with many of the extremes given varietal status by many authors. However, after careful analysis of our material, delimiting varieties on such characters as leaf width, peduncle length and width of appendages is unacceptable because variation on an individual plant would, in most cases, incorporate the spectrum of the varieties. With this in mind and until further work is done over the entire range of species, I have not separated any of the varieties other than the pubescent form.

15b. **Euphorbia corollata** L. var. **mollis** Millsp.

HABITAT: The same as that given for var. *corollata.*

RANGE: Southeastern fourth, northeastern corner of Kansas and adjacent southeastern Nebraska with a single collection from southeastern South Dakota. Map 10.

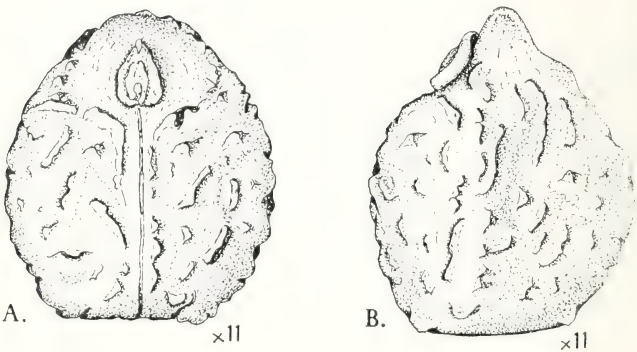
The collection from Clay Co., South Dakota, appears to be an extension of the range to the north. However, the collector (W. H. Over, July 20, 1925) gives the following information on the sheet: "Growing by introduction in my yard in Vermillion, but never found native to my knowledge."

In var. *mollis*, the amount and type of pubescence tends to vary considerably from plant to plant. Some plants may possess a dense, almost woolly type of pubescence with other plants being virtually glabrous. Still other plants may have completely glabrous stems, but the leaves will be variously pubescent. Steyermark (1963) and Gleason (1952) both make the comment that the pubescence appears to be a response to the environment, with the more pubescent plants found in drier exposed situations. From personal collections in our area, however, this does not appear to be very valid since both pubescent and glabrous forms were collected in the same area and, in most cases, in the immediate vicinity of each other. Several collections were taken from relatively dry prairie situations while others were taken from relatively moist roadsides and weedy areas along small streams. In general, it may be that the environment does play a definite role in the manifestations taken by this species, but the real interpretation of the variations rest in field and experimental studies.

16. **Euphorbia dentata** Michx. Fl. Bor. Am. 2: 211. 1803.

Euphorbia dentata (var.) *cuphosperma* Engelm., Rep. U.S. & Mex. Bound. Surv. 2: 190. 1859. Type: *Wright 1834* (MO!).
Euphorbia cuphosperma (Engelm.) Boiss., DC. Prod. 15 (s): 73. 1862.
Poinsettia cuphosperma (Engelm.) Small, F. Southeastern U.S. 721, 1334. 1903.
Euphorbia dentata forma *cuphosperma* (Engelm.) Fern., Rhodora 50: 148. 1948.

Fig. 18



Euphorbia dentata Michx.

FIG. 18. *Euphorbia dentata.* A. Raphial view of seed. B. Side view of seed with raphe on the left.

Annual; erect or ascending, 15-50 cm tall, usually densely branched from near base, stems with 2 types of vesture present, puberulent evenly over stem with larger more prominent strigose to hispid hairs scattered throughout; leaves opposite (rarely alternate), scabrous above, strigose-hispid below, leaves ovate to linear-lanceolate, or orbicular-oblong to rhombic-ovate, 1-9 cm long, 0.2-5.0 cm wide, margin dentate to subentire, base cuneate, upper and bracteal leaves usually pale at base; petiole strigose-hispid, up to 3 cm long; stipules glandlike; cyathia in congested axillary or terminal cymes; involucres nearly sessile, campanulate, to 3 mm long, essentially glabrous both inside and outside; lobes oblong, sharply dentate to fimbriate, surpassing gland(s), folding in over summit of involucre; glands 1 or more commonly 2, with central involucre rarely having full compliment of 5, fleshy, sessile, flattened obconical to tangentially bilabiate, light to dark green; appendages absent; bracteoles forming partial radial partition between fascicles of staminate flowers, fused basally for ½ length, dissected above into 2-5 linear segments, pubescent along margin, equaling to rarely exceeding summit of involucre; staminate flowers 5-8 per fascicle, 25-40 per involucre; styles 1.0-1.5 mm long, bifid ½ length; mature capsule 3-5 mm long, 4-5 mm wide, glabrous to slightly strigose; seeds 2.5-3.0 mm long, 2.0-2.5 mm broad, ovoid to globose, sharply angled, rather finely and sharply tuberculate, caruncle flat, coat white to brown or black. Fig. 18.

Habitat: Moist to dry soils in areas of major disturbance such as roadside ditches, margins of cultivated fields, waste places and railroad embankments. Usually occurs in large colonies where found.

Range: Common over Kansas, southern one-half and eastern portions of Nebraska, and southern South Dakota. Map 11.

In our area this species is extremely variable particularly in leaf form. In most cases, the various extremes in leaf form have been given both varietal and form rank or even elevated to species rank. The most commonly recognized variation in our area is the narrow-leafed form. Harrington (1964) indicates var. *cuphosperma* from our area and separates it mainly on the narrower leaves, pubescence of the capsule, and seed shape. Steyermark (1963) separates forma *cuphosperma* only by leaves at summit of stem and main nodes as being linear to narrowly lanceolate.

Fernald (1948) in reducing var. *cuphosperma* to a form, makes the statement that the transition from the linear or narrowly-lanceolate form is gradual with the distinctions in the seed completely failing.

Examination of material revealed that the narrow-leaved form in its extreme form could be recognized, but the intergradation to the typical broad-leaver form was complete and in many cases occurred in the same population. The character of strigose capsules in the narrow-leaved form versus the glabrous capsules in the typical form completely failed in that many plants with capsules which were immature possessed a strigose type of pubescence. However, as the capsule matured, the pubescence evidently dehisced since most of the mature capsule on the same plant were glabrous. In cases where several stages of the capsule development could be observed on the same plant, a gradual decrease in the amount of pubescence could also be seen. In addition, the presence of pubescence was very sporadic throughout our area with no geographic correlation, and in most instances little environmental correlation could be drawn.

With the points mentioned above, along with no correlation in seed shape, it seems rather hopeless to separate the species into varieties based only on the general morphology of the plants. Dressler (1961), however, has indicated some cytological evidence correlated with morphology to show a clinal pattern of variation to the north from central Mexico, into Arizona and western Texas. Perhaps a more thorough investigation of plants in that area will lead to a better understanding of the forms in our area.

17. **Euphorbia cyathophora** Murr., Comm. Gotting. 7: 81. 1786.
Euphorbia heterophylla var. *graminifolia* Engelm., Rep. U.S. & Mex. Bound. Surv. 2: 190. 1859.
Poinsettia cyathophora (Murr.) Kl. & Gke. Monatsb. Akad. Berlin 1859: 253. 1859.
Euphorbia heterophylla L. most American authors.

Annual; erect, to 1 m tall, essentially glabrous or with few scattered hairs on stem, particularly at nodes; leaves usually of 2 basic forms, cauline alter-

Map 11

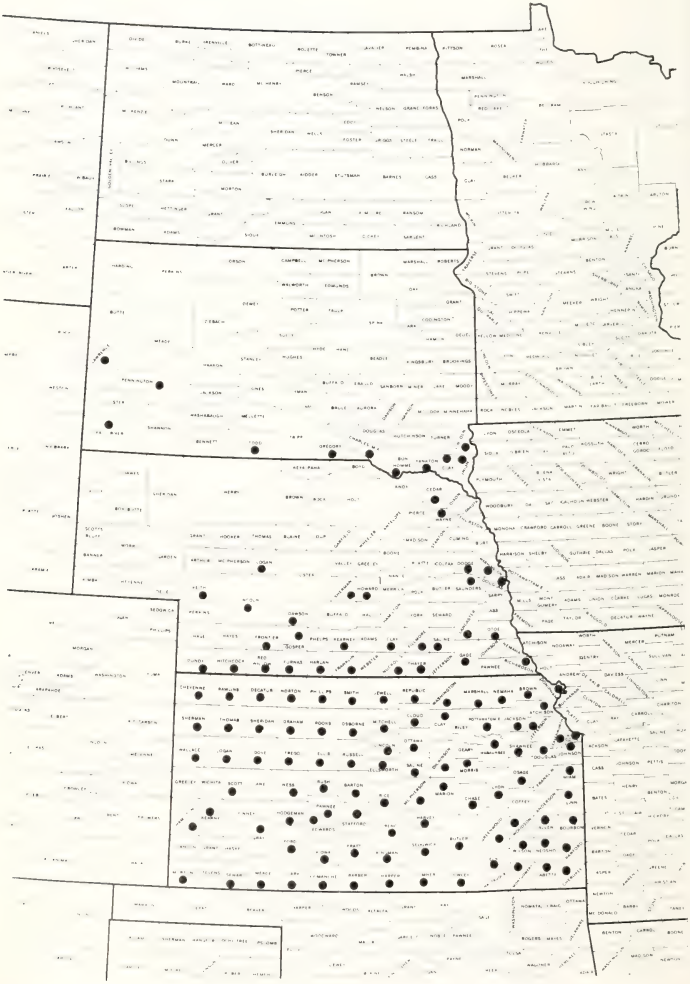
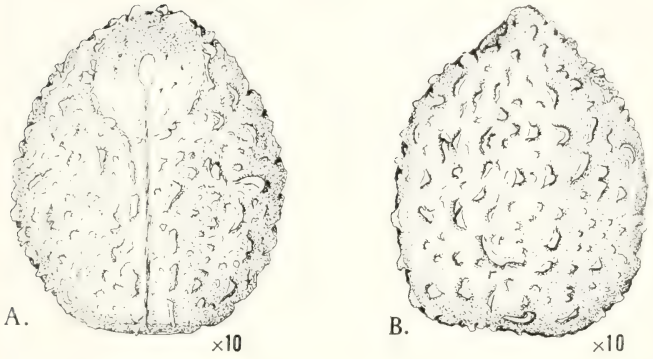


Fig. 19



Euphorbia cyathophora Murr.

Fig. 19. *Euphorbia cyathophora*. A. Raphial view of seed. B. Side view of seed with raphe on the left.

nate, mostly unlobed, linear or narrowly lanceolate to oblong or ovate, uppermost and bracteal leaves opposite or alternate, variously lobed to oblong, elliptic or panduriform, typically with prominent red base. Leaves 2-13 cm long, 0.1-7.0 cm wide, glabrous or slightly pubescent below primarily along veins, tapering equally to petiole, margin entire or serrate to lobed; stipules gland-like; inflorescence usually terminating stem or branches with a many rayed umbel; involucres sessile or with petiole to 3 mm long, broadly campanulate, 2-5 mm long, glabrous both inside and outside; lobes broad, apex fimbriate, glabrous, surpassing gland(s), folded over summit of involucre; glands 1 (rarely 2), broad, more-or-less bilobiate, opening narrowly oblong, 0.7-1.5 mm long; appendages absent; bracteoles forming broad partition between fascicles of staminate flowers, fused for ½ length, dissected above into linear segments, not exceeding summit of involucre, short pubescent along margins of segments; staminate flowers 5-11 per fascicle, 30-50 per involucre; styles ca. 1.0 mm long, bifid for over ½ length; capsule 3-4 mm long, 6-8 mm wide, glabrous; seeds 2.5-3.0 mm long, 2.5-3.5 mm wide, oblong, ovate, to subglobose, inflated, not angular, finely and sharply tuberculate, caruncle usually absent, coat reddish brown to black with tips of tubercules lighter in color. Fig. 19.

HABITAT: Primarily moist loam of open woods, river banks or shaded areas. Occasionally as a weed of waste places or areas of mild disturbance.

RANGE: Eastern and north-central Kansas; south, east, and north-central Nebraska; extreme southeastern South Dakota. Map 12.

Dressler (1961) indicated that the name *E. heterophylla,* as applied by most American authors, is applicable to a South American species more often labeled *E. geniculata* or *E. elliptica.* Apparently the confusion has been the identity of Linnaeus' *Euphorbia heterophylla.* Most workers felt that the epithet applied to the familiar North American plant with red and green floral bracts. Consequently, due usually to a very superficial observation, both the Central and North American forms were simply identified as *E. heterophylla* with most of the South American material identified as *E. geniculata* or *E. elliptica.*

However, as Dressler *(loc. cit.)* points out, the epithet of Linnaeus refers to the shape of the leaves and not color. Since there was no specimen of *E. heterophylla* in the Linnaean Herbarium, Dressler resorted to the work of Plukenets which shows a plant with both lanceolate and pandurate leaves; this appeared to be more characteristic of the tropical form with green floral bracts. With further investigation, it was shown that the North American entity differed rather consistently from the tropical form and, therefore, applied the name *E.* (*Poinsettia* of Dressler) *cyathophora* Murr. to the plant of North America. Further investigation revealed that the tropical form with green floral bracts was more characteristic of the epithet as to leaf shape as described by Linnaeus.

Basically, *E. cyathophora* possesses floral bracts which are usually red, with gland bilabiate or with a transversely elongate opening, seeds finely and sharply tuberculate and not angular. *E. heterophylla* has floral bracts green or pale basally (never red), gland(s) narrow, substipitate with circular opening and seeds coarsely and bluntly tuberculate and angular.

18. **Euphorbia spathulata** Lam. Enc. Mêth. 2: 428. 1788.
Euphorbia dictyosperma Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 37. 1836.
Euphorbia arkansana Engelm. & Gray, Plantae Lindheimer in Bot. Journ. Nat. Hist. 5: 53. 1845.

Annual, rarely biennial; ascending to erect, 20-45 cm tall, glabrous; cauline leaves alternate, glabrous, oblanceolate to spatulate, 10-30 mm long, 2-20 mm wide, apex obtuse, margin serrulate, particularly from widest point to apex, base truncate to subcordate to slightly clasping stem, sessile to shortly petiolate near base of plant; floral leaves and bracts opposite, round ovate to oblong, 1.0-2.5 mm long, sessile; stipules absent; inflorescence umbelliform with ray dichotomously branched several times; peduncles sessile to 3 mm long; involucres broadly campanulate, ca. 1.0 mm long, glabrous both inside and outside; lobes ovate, shallowly lobed, equaling to slightly surpassing glands, but usually inconspicuous due to folding into mouth of involucre; glands 4

Map 12

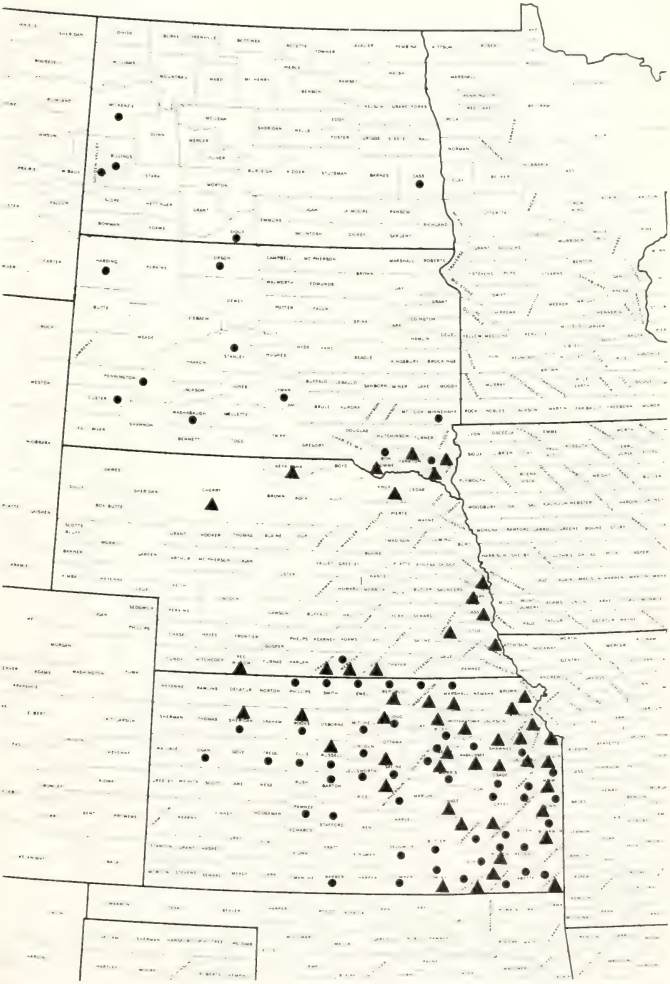
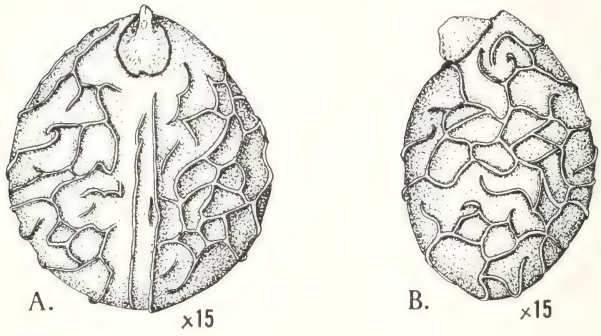


Fig 20



Euphorbia spatulata Lam.

FIG. 20. *Euphorbia spathulata*. A. Raphial view of seed. B. Side view of seed with raphe on the left.

(rarely 5), elliptic to transversely oblong, not horned, 0.5-0.1 mm long, yellow, sessile; appendages absent; bracteoles reduced to rather broad appendage between staminate flowers, basally adnate, fused with involucre basally, apex entire to shallow lobed or incised; staminate flowers 1-2 per fascicle, 5-8 per involucre; styles slender, ca. 1.0 mm long, bifid for about ½ length, spreading and recurved; capsules 2.2-3.0 mm long, 2.5-3.5 mm wide, glabrous, verrucose to tuberculate, with conical to cylindrical papillae ,particularly near apex and on angles of capsule, bent toward apex; seeds 1.4-2.0 mm long, 1.2-1.5 mm wide, 0.9-1.1 mm wide tangentially, seeds radially ellipsoid or ovoid, tangentially lenticular ovoid or flattened, coat brown to black with sharp fine reticulated or wrinkled surface. Fig. 20.

HABITAT: Moist sandy soil of open woods, mesic ditches, along roadside and railroad embankments to grazed prairie pastures.

RANGE: Primarily eastern two-thirds of Kansas with scattered collections in western one-third, primarily from northern and southern counties; one collection from south-central Nebraska (Webster Co.); scattered collections from primarily the western one-half of the Dakotas. Map 12.

There has been much disagreement as to the proper name for this species. Norton (1900) distinguished the plant from the European species and applied *E. arkansana* Engelm. & Gray. However, more recent authors do not con-

sider it distinct and include our material under the more familiar name *E. dictyosperma* Fisch & Mey.

In addition, Croizat (1943), stated that he could not find any differences between *E. spathulata* and *E. dictyosperma* and listed the latter in synonomy under *E. spathulata.* I also found this to be true.

Although most manuals (Rydberg, 1932, Gates, 1940, and others) list the closely allied species *E. obtusata* as occurring here, I have excluded this species since material examined has been identified as *E. spathulata.* However, in trying to delimit the two species, a problem as to identification of each entity was encountered.

Steyermark (1963), in his discussion of *E. spathulata,* indicates that the gland coloration distinction between the two species (red or scarlet in *E. obtusata,* yellow in *E. spathulata*) and the presumed difference of floral leaves (cordate-clasping in *E. obtusata,* truncate to subcordate at base in *E. spathulata*) cannot be relied upon to separate the two taxa in Missouri. As to *E. spathulata* in our area, I also found this to be true since all of the afore-mentioned characters could be distinguished on the one rather variable species, with many of the same characters present on *E. obtusata* from other areas. In addition, I found that the distinctions which supposedly occur in the glands did not hold true for the one species in this region. In *E. obtusata* all five glands are present with *E. spathulata* having four glands, the fifth being replaced by a tuft of hairs or a small lobe (Steyermark, 1963). In examination of *E. spathulata,* I found that many of the involucres contained the full compliment of five glands, those with only four having a deep broad sinus with no indication of a tuft of hairs.

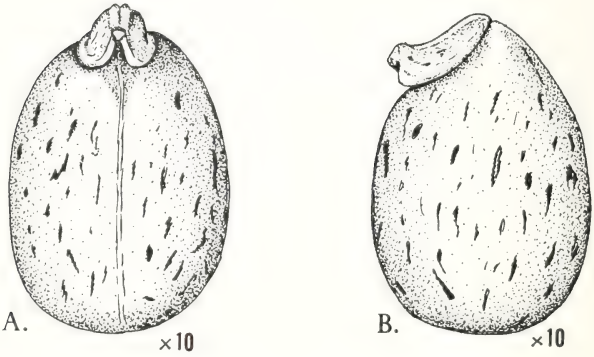
Moreover, the seed length was found to be rather unreliable in many cases. Steyermark (1963) and Gleason & Cronquist (1963) list *E. spathulata* as having seeds 1.3-1.5 mm long while Gleason (1952) lists the length as 1.5-1.8 mm long. Harrington (1964), however, gives the length as 1.5-2.0 mm which was found to be the size of seed material examined here. Examination of *E. obtusata* revealed a considerable amount of overlap with *E. spathulata* since the former is listed as having seeds 1.7-2.0.

The character I found to be the most reliable and the one I mainly used to distinguish the species was reticulations on the seed, with *E. spathulata* having prominent and sharp reticulations or wrinkles and *E. obtusata* with seeds smooth or obscurely reticulate.

From the material examined, the status of these two species appears to be in doubt with definite indications for thorough study of the two over their entire range.

19. **Euphorbia podperae** Croiz. Amer. Midl. Nat. 37: 801. 1941.
E. intercedens Podp. in Publ. Fac. Sc. Univ. Masaryk 12: 29. 1922; Domin, Pl. Cecosl. En. 77. 1935—not *E. intercedens* Pax. in Engl. Bot. Jahrb. 34: 75. 1905.
E. esula L. (of most American authors).

Fig 21



Euphorbia podperae Croiz.

FIG. 21. *Euphorbia podperae*. A. Raphial view of seed. B. Side view of seed with raphe on the left.

Perennial; erect, 40-90 cm tall, glabrous, branches immediately below umbel usually fertile, branches toward base usually sterile and densely leafy, stems single or several, scaly below; principal cauline leaves scattered, 30-75 mm long, 2-10 mm wide, broadly oblong-linear to lanceolate; leaves subtending umbel whorled, 10-20 mm long, 1-10 mm wide, ovate-lanceolate to oblong-ovate; floral bracts opposite, 10-20 mm long, 5-15 mm wide, reniform-cordate to deltoid-cordate; stipules absent; inflorescence umbelliform 7-12 rayed with each ray dishotomously branches 1-3 times; peduncles up to 3 mm long; involucre campanulate to obconical, 1.5-3.0 mm long, glabrous outside, puberulent inside on lobes; lobes broad, apex emarginate to obtuse, densely pubescent inside and along margin, equaling glands; glands 4, crescent shaped, rarely denticulate, 1.5-2.0 mm long; appendages absent; bracteoles forming slender partition between fascicles of stamens, apex dissected into several linear segments, glabrous to slightly pubescent at apex, equaling involucre in length; staminate flowers 3-5 per fascicle, 15-25 per involucre; gynophore usually long exerted, mature capsule exerted as much as 1 cm beyond involucre, straight to reflexed; styles 1.5-3.0 mm long, bifid for ¼ length; capsule 2.5-3.5 mm long, 3.5-4.5 mm wide, minutely regulose along either side of suture, particularly near base; seeds 2.2-3.0 mm long, 1.2-1.7 mm

wide, oblong-cylindrical, coat smooth, brown or silver-gray to white, typically mottled, caruncle large, flat. Fig. 21.

Habitat: Moist to dry sandy thin soils of roadsides and railroad embankments, waste areas and margins of cultivated fields.

Range: Common over most of North Dakota; scattered over northeastern, southeastern and west-central South Dakota (Black Hills region); southern one-half of Nebraska, with four collections from Kansas (Greenwood, Marion, Marshall, and Washington Counties). Map 13.

As anyone familiar with this complex realizes, the names that have been applied to it have been the subject of a voluminous amount of literature and information both in this country and to a greater extent in Europe. Consequently, only information pertinent to the variability of the plants found in our area will be discussed or, in some instances, information needed for sake of clarity.

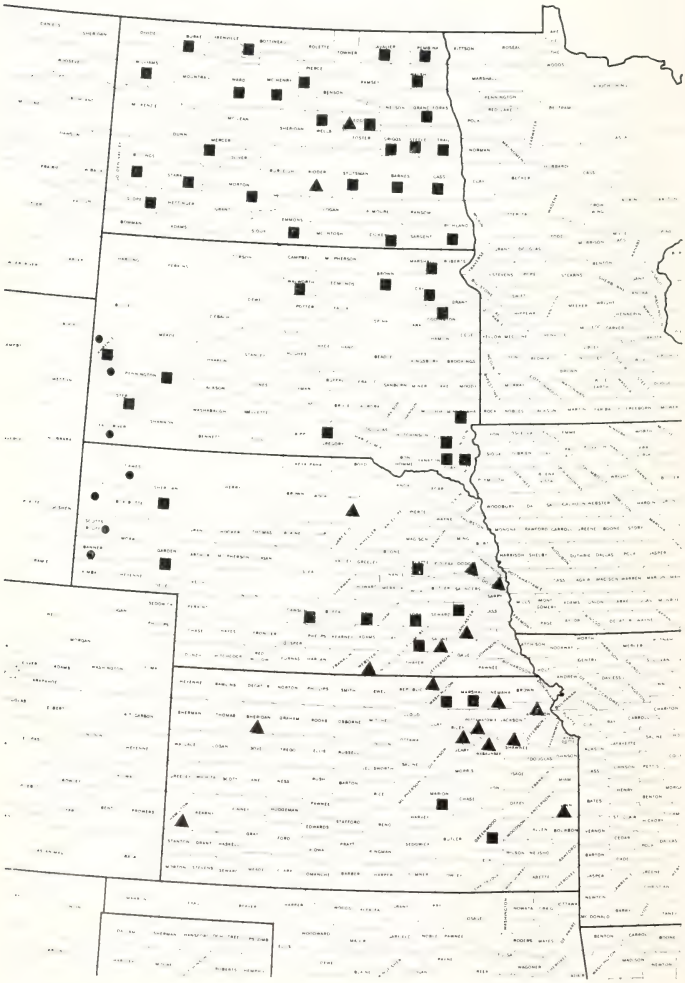
Most conservative American authors have not separated the plants collected in this country from *E. esula* L. of Europe. However, Morton (1937) stated that he had not seen any specimens of *E. esula* from the United States and concluded that the plants of the U.S., particularly those of the Midwest, should be *E. virgata* Wald. & Kit.

Wheeler (1939) concluded that *E. virgata* was not distinguishable from *E. esula* and maintained that our material should be identified as *E. esula* L. In addition, he points out that *E. virgata* Wald. & Kit. is actually preoccupied by *E. virgata* published earlier by Desfontaine for another plant.

Croizat (1945) reviewed all previous work and investigated virtually all previous aspects of the *esula-virgata* complex with some rather significant conclusions. However, due to the complexity and involvement of his reasoning, no attempt will be made here to summarize his work but rather refer readers to his entire publication which would be better understood in its entirety.

Croizat (*loc. cit.*), however, does not drop *E. virgata* of Wald. & Kit., as would be indicated by Wheeler's findings. Rather, he substantiates with limitations the acceptance of *E. virgata*. In addition, he considers Morton correct in his assumption that *E. esula* of Linnaeus has not been found in this country although it may well be expected in parts of Washington, Oregon, and British Columbia due to the type of climate existing there in comparison to where found in Europe. However, Croizat does not agree with Morton in assuming that the plant of the Midwest is *E. virgata* since specimens examined indicate *virgata* to be a ballast-plant from the East coast (Boston). Croizat then suggests the plant of the Midwest should be *E. intercedens* as indicated by a collection of Palmer from Massachusetts which matches the one described by Podpera from Czechoslovakia. In a later publication, however, Croizat (1947) states that Palmer has informed him that *E.*

Map 13



intercedens Podp. was preoccupied by *E. intercedens* Pax. (in Engl. Jahrb. 34: 75. 1905.) and, consequently, Podpera's name must be rejected. With this in mind, Croizat proposes *Euphorbia podperae* Croiz. as the name that should be applied. In applying an entirely new name, Croizat states that it can be used as a reference for American taxonomists with the assurance that it can be connected to specimens deposited in well-known herbaria.

Since Croizat has delved rather deeply into the subject of the "*esula* complex," I have followed his recommendations even though in many cases Croizat himself feels they are only provisionary, pending a study of the group on a world-wide basis.

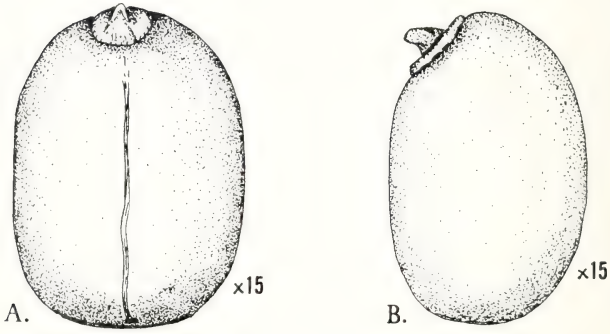
20. **Euphorbia cyparissias** L. Sp. Pl. 1: 461. 1753.

Perennial from extensively creeping and branched rootstock; stems single to numerous, 10-30 cm tall, glabrous, branches immediately below umbel fertile, branches toward base usually sterile, densely leafy, with longer branches usually overtopping inflorescence; principal cauline leaves scattered, 10-30 mm long, 0.5-3.0 mm wide, narrowly linear to linear-filiform or linear-spatulate to oblong-lanceolate; leaves subtending umbel whorled, 4-15 mm long, 1-5 mm wide, lanceolate; floral leaves and bracts opposite, 4-6 mm long, 4-10 mm wide, reniformcordate to broadly ovate, yellowish to purple or red; stipules absent; inflorescence umbelliform, 10-20 rays, each ray dichotomously branches 1-3 times; cyathia sessile to very short pedunculate, involucres turbinate to campanulate, 2-3 mm long, glabrous outside, slightly pubescent inside beneath gland and summit of involucre; lobes broadly oblong with apex entire to broadly ciliate at apex and along margin, noticeably exceeding glands; glands 4, lunate to semi-crescentric, 1.2-1.5 mm long, horns short and divergent, waxy yellow; bracteoles reduced to small linear appendages, slightly exerted beyond summit of involucre; staminate flowers 1-3 per fascicle, 5-18 per involucre; styles 0.5-1.0 mm long, bifid for less than $\frac{1}{4}$ length; mature capsule 2.0-2.5 mm long, 2-3 mm wide, glabrous, smooth to slightly rugulose along sides of suture; seeds ca. 2 mm long, 1.0-1.5 mm wide, oblong-cylindric, smooth, coat brownish-gray to silver white, caruncle flattened with raised center. Fig. 22.

HABITAT: In general, escaping from cultivation and becoming naturalized along roadsides, old and neglected fields and waste areas. Many of the collections record collections from old flower beds or near deserted homes and farms, with a large majority of the specimens from old neglected cemeteries.

RANGE: Primarily northeastern Kansas and southeastern Nebraska and South Dakota, with collections very scattered in western Kansas, central Nebraska and North Dakota. Map 13.

Fig. 22



Euphorbia cyparissias L.

FIG. 22. *Euphorbia cyparissias*. A. Raphial view of seed. B. Side view of seed with raphe on the left.

Although this species is extremely variable, it is seldom confused with any other except perhaps the sterile, narrow-leaved form of *E. podperae* (*E. ersula* of most authors) which it resembles very closely.

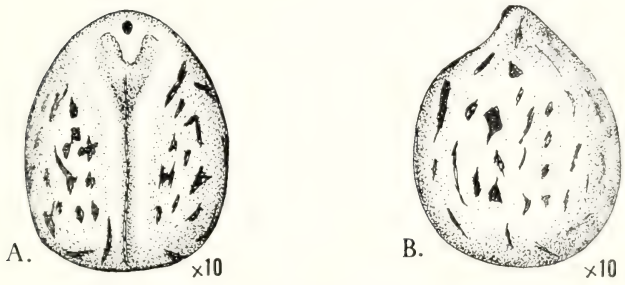
From collection data, the sporadic distribution of this species appears to be due to its extensive cultivation in flower and rock gardens or cemeteries. It evidently escapes and becomes naturalized along roadsides or cultivated fields. Steyermark (1963) comments that this species can become a serious weed if not checked, due to the underground, creeping and extensively forking rootstock. If allowed to become established in an area, it will usually spread rapidly and form extensive colonies.

From observations of herbarium material, this species apparently produces very few seeds. Some specimens bear no capsules while others have no more than six. Each capsule produces no more than one or two seeds.

21. **Euphorbia robusta** (Engelm.) Small *in* Britt. & Brown, Ill. Fl. 2: 381. 1897.
E. montana robusta Engelm. Mex. Bound. 2 (1): 192. 1859.
E. montana Engelm. Mex. Bound. 2 (1): 192. 1859.

Perennial; erect to decumbent, 10-30 cm tall, glabrous, branches spreading; cauline leaves alternate, 7-16 mm long, 4-15 mm wide, narrowly lanceolate to oblong or oblong-ovate; leaves subtending umbels whorled, little different from cauline; floral bracts and leaves broadly ovate to cordate to tri-

Fig. 23



Euphorbia robusta (Engelm.) Small

angular-ovate or subreniform; stipules absent; inflorescence umbelliform, 3-5 rayed with each ray dichotomously branched several times; peduncles up to 1.0 mm long; involucres broadly campanulate 2.0-2.5 mm long, glabrous outside, slightly pubescent inside at summit; lobes triangular or triangular-lanceolate, apex entire to bidentate, hirsute on inner surface, surpassing glands; glands 4, crescent-shaped to semilunate, horns short, rarely dentate between horns, 1-2 mm wide, 1.0 mm or less long, pubescent inside on short stipe; appendages absent; bracteoles short, narrow, fused basally, dissected above into 2-3 linear segments, pubescent on margins; staminate flowers 2-3 per fascicle, 10-15 per involucre; styles 0.5-1.0 mm long, bifid for ½ length; mature capsule 4.0-4.5 mm long and wide, glabrous, long exerted 4-5 mm beyond summit of involucre; seeds 2-3 mm long, 1.4-1.7 mm wide, ovoid, low rounded ridges down dorsal dise of seed, coat gray or brown, smooth or with shallow irregular depressions or pits, caruncle low conical, soon deciduous. Fig. 23.

HABITAT: Dry sandy to rocky upland prairies or sides of bluffs and ridges.

RANGE: Extreme western Nebraska and South Dakota. Map 13.

This species barely extends into our region from the west. From a limited amount of material studied, this species appears to produce very few seeds with many of the capsules bearing only one or two seeds, very rarely three.

SPECIES EXCLUDED FROM STUDY REGION

E. agraria=*E. podperae*

E. lucida=based on specimens in KSC, *Dodd 111 & Neff s.n.*, 1936, from Washington Co.,=*E. podperae* Croizat. Two-page note attached to sheet by L. Croizat sent to herbarium in 1942 indicates that *E. lucida* W. & K. should be excluded and he tentatively identified specimen as *E. intercedens* Polp. In 1947, however, he changed his name to *E. podperae* Croiz. (see discussion of *E. podperae* for explanation).

E. obtusata=all material seen from area=*E. spathulata* or otherwise identified.

*E. vermiculata*listed from Crawford Co., Kansas, *Gibson 1963*. Specimen not seen but range is to the east.

FLORISTIC RELATIONSHIPS

An analysis of the distribution of *Euphorbia* in North America north of Mexico has yielded the following information: Of the 21 species occurring in the four-state region, 13 range both east and west of the Mississippi River with the remaining 8 species found only west of the Mississippi River. Only 3 of the species are considered introduced in our area; but in all cases, the species have become naturalized. *E. prostrata* is native to tropical America from South and Central America to Mexico and the West Indies. Both *E. podperae* and *E. cyparissias* are perennials introduced from Europe, with *E. podperae* usually listed as a troublesome weed if not controlled.

Four other species are perennial, but all are native. *E. fendleri* and *E. lata* are definitely associated with the southern and western floras and apparently reach the northern and eastern limits of their range here. *E. robusta* only extends into the west-central portions and appears to be the eastern extension of the range from Colorado, Wyoming and Montana. The remaining perennial, *E. corollata* is a wide ranging eastern species and enters the four-state region primarily from Missouri and Arkansas.

The other 15 species are annuals and native. As stated by Wheeler (1941) in reference to the subgenus *Chamaesyce*, the main centers of distribution, based strictly on the numbers of species present, would appear to be the southwestern portions of the U.S. Wheeler gives Pima Co., Arizona, and the Big Bend area of Texas as containing the largest number of species for an area with a radius of 50 miles. Of the 47 species in Arizona listed by Kearney & Peebles (1951) only 13 are found in the four-state region, while Gould (1962) lists 62 species from Texas, 20 of which are found here. Of the 62 species listed from the southeastern U.S. by Small (1933), only 11 are found here; and of the 30 species given by Abrams (1951) in the Pacific States region, only 8 are present in our area.

A further comparison of the four-state region with manuals of adjacent or closely-related areas (Steyermark, 1963; Fernald, 1950; Gleason & Cron-

quist, 1962; Harrington, 1964) indicate a rather close floristic relationship with the Texas and Oklahoma regions. The relationship apparently is even closer than to areas immediately adjacent to the west or east. A migration of *Euphorbia* into our area is indicated primarily from the south and southwest with a few species extending in from the eastern and western regions.

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The Taxonomy of the Genus *Echinacea* (Compositae)

RONALD L. MCGREGOR
Botany Department
University of Kansas

ABSTRACT

The North American genus *Echinacea* consists of nine species and two varieties and has a distribution centering in Arkansas, Oklahoma, Missouri, and Kansas. *E. pallida* is a segmental allopolyploid, and *E. angustifolia* var. *strigosa* includes both diploid and tetraploid populations. All taxa will hybridize when brought together and frequent hybrids are found in nature. Introgression is found between *E. atrorubens, E. angustifolia* var. *strigosa, and E. a.* var. *angustifolia* and is responsible for much of the variation in *E. angustifolia*. *E. pallida* and *E. angustifolia* are a source of the drug echinacin and variants of *E. purpurea* are useful cultivars.

INTRODUCTION

The North American genus *Echinacea* is native to the Atlantic drainage area of the United States, extends into Canada, but is unknown from Mexico. Species appear to be adventive in New England, rare in the Great Lakes region, very scattered at elevations above 4500 feet toward the Rocky Mountains, and have not been found in New Mexico, southern Texas, and Florida.

The morphological variability within this genus has led to much disagreement in the treatment of taxa as noted by Fernald (1900), Boynton and Beadle (1901), Palmer (1936), Cronquist (1945), and Dress (1961). The only taxonomic treatment of the genus was included in the work of Sharp (1935), but this was in no way comprehensive, and his exclusion of one species only added to existing confusion.

While the species are relatively distinct from one another, specific differences are narrowly defined. All taxa will hybridize when brought together and considerable natural hybridization occurs. One species is a segmental allopolyploid, and one variety includes both diploid and tetraploid colonies.

These situations, along with the fact that major herbaria contained insufficient material for adequate study, no doubt have been responsible for most of the difficulties.

During the past 15 years, I have made field studies throughout the range of the various species. Several hundred transplants representing all species were grown in the experimental garden and greenhouse for a period of eight years, and several thousand plants were grown from seed both in the garden and in the greenhouse.

All possible combinations of crosses were attempted, and many back-crosses were completed. Chromosome counts were made from over 2100 field collections of buds, root tips from transplants, and root tips from seed.

The following studies were conducted to help elucidate the interrelationships and status of all taxa and to present a better understanding of the genus.

ACKNOWLEDGEMENTS

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ECONOMIC IMPORTANCE

The history of *Echinacea* species as drug plants is interesting and follows much the same pattern as others in that it has had its periods of favor and disfavor. Dr. H. C. F. Meyer of Pawnee City, Nebraska, first introduced the drug in 1885 (Lloyd, 1923) after having learned of its use by the Indians. He sent a bottle of his "Meyers Blood Purifier" to Prof. John King of Cincinnati and roots for identification to Mr. J. U. Lloyd of the Lloyd Brothers Pharmaceutical Company, Cincinnati. In 1886 Dr. Meyer submitted a whole plant to Lloyd Brothers where it was identified as *Echinacea angustifolia* DC.

Dr. Meyer made extravagant claims for his drug as evidenced by the label he prepared in 1886: "This is a powerful drug as an alternative and antispectic in all tumorous and syphilitic indications; old chronic wounds, such as fever, sores, old ulcers, carbuncles, piles . . . can be cured quick and active . . . . It will not fail in gangrene. In fever it is a specific; typhoid can

be adverted in two or three days . . . . It cures bites from the bee to the rattlesnake . . . . It has cured hydrophobia . . . ."

These extravagant claims strongly prejudiced Lloyd Brothers against *Echinacea*. However, Prof. King decided to make a therapeutic investigation and soon became personally interested in the drug as tincture of echinacea appeared to be a palliator in the treatment of Mrs. King's virulent cancer. By 1887, Prof. King was so convinced of the drug's value through his investigations that he announced its value in the same year in the Eclectic Medical Journal. Once announced to the Medical Profession, the drug soon became known from coast to coast and the demand forced Lloyd Brothers to go into production. Sayre (1915) reported that thousands of pounds of *Echinacea angustifolia* root were shipped out of Kansas each year. Lloyd (1923) reported that the echinacea drug was the most used American drug introduced since 1885. At this time Lloyd was actively advertising the drug on behalf of Lloyd Brothers. The spokesman for the Medical Profession, however, had soundly renounced the drug as the editor of the Journal of the American Medical Association (Nov. 27, 1909, p. 1836) wrote "In view of the lack of any scientific scrutiny of the claims made for it, echinacea is deemed unworthy of further consideration until reliable evidence is presented in its favor." Thus, even though the drug was renounced, it was prescribed by many physicians until its use nearly disappeared in the late 1920's. My check of several pharmacies in 1958-60 revealed that some still stocked tincture of echinacea which was purchased by some people as a blood purifier. The digging of the root for crude drug companies was much curtailed but has never ceased.

During the 1940's and 50's interest in research on *Echinacea* developed. Hartzell (1947) reported that an acetone extract of *Echinacea* species killed 50% of the larvae of the mosquito *Culex quinquefaciatus* at a concentration of 1000 p.p.m. or less. Hepburn *et al.* (1950) reported an experiment in which each of six human subjects ingested 8 minims of tincture of *Echinacea angustifolia* daily for 13 days. Excessive thirst and perspiration resulted; blood sugar fluctuated as much as 20 mg.; chlorides as much as 55 mg.; blood cholesterol first increased, then dropped to normal or even subnormal levels. Stoll *et al.* (1950) reported that a water soluble crystalline compound (echinacoside) was isolated to the extent of about 1% of the root and was weakly active against *Staphylococcus aureus* and streptocci. Koch (1953) reported that pretreatment of guinea pig subcutaneous tissue with echinacin causes a retardation and localization of streptococci infection.

As research continued, a sudden demand for *Echinacea* root developed in 1965 with orders placed for all the root that could be obtained and one supplier of crude drugs organized a large scale program, resulting in the production of over 25,000 pounds of dried root in one year. At this time it

was apparent that *Echinacea pallida* was the species most desired though *Echinacea angustifolia* was acceptable. Research during this time has been clothed in secrecy, and the future of the drug remains uncertain for in 1967 the demand for the root decreased.

Horticulturally, *Echinacea* species are of some value, and it appears the full possibilities have not been explored. Seed companies offer seed of *Echinacea purpurea* often under the name *Rudbeckia purpurea*. The wild form is considered to be an inferior garden plant but is sold by horticulturalists on a limited scale. A few improved forms are offered in the United States under the names "the King," "Sombrereo" and hybrid mixtures. These have been selected and do not show evidence of any hybrid origin. A number of German cultivars have been developed with green disks, white or greenish rays, and yellow, orange-tipped paleae and are listed under the names alba, white Prince, White Lustre, and white King. All these variants have been observed in native wild stands. A large cultivar has existed in England under the name New Colewall Strain of *Echinacea*. This features heads up to six or seven inches in diameter with the cone center greenish-bronze and later becoming shades of copper or red. A tendency toward this variant also has been observed in native wild colonies.

Evidence indicates the best possibility for obtaining a new valued cultivar is in the hybrids between *Echinacea purpurea* L. and *E. angustifolia* DC. var. *angustifolia*. These hybrids form a rather compact, rounded bushy plant about 2 feet in diameter. It is well adapted to growth in full sunlight, tolerates a variety of soil conditions, and has a long flowering period. It is winter hardy and drought resistant, at least in Kansas.

COMPARATIVE ANATOMY

During this investigation of *Echinacea*, Keller (1962) and I were able to study the general anatomy of all taxa except *E. tennesseensis*. These investigations revealed nothing new for the Compositae, but a number of characters were found to be taxonomically significant and useful in distinguishing some species and varieties.

Studies of the petiole revealed that in *E. simulata* the median vascular bundle is fan-shaped in transection, while all others are round. Brachysclerids or stone cells were isolated to clustered in the petiole of *E. paradoxa* var. *neglecta* but were found nowhere else in the genus. In *E. atrorubens* the petiole has air spaces or canals running the entire length of the petiole while in all other species they are found only near the base of the petiole.

The anatomical studies of the stem revealed few characters of value, though detailed studies of secondary growth, relative abundance of tissues, and cell wall thickness often show differences among the species. A few characters, however, are readily useful. In *E. angustifolia* var. *angustifolia*

and var. *strigosa* the pith always has sclerenchyma fibers scattered throughout. These are absent in all other species. These varieties, however, lack secretory canals in the pith which occur in all other taxa.

Anatomical studies of the ligule have revealed characters of taxonomic value even in distinguishing varieties of a species. In *E. purpurea* a transection of the ligule reveals 29 to 31 veinlets while all other species have 12 to 16. The closely related *E. laevigata* lacks secretory canals in the ligule while in *E. purpurea* they are very evident. *E. simulata* and *E. pallida* have secretory canals in the ligule but the closely related *E. sanguinea* does not. The secretory system in the ligules of *E. paradoxa* var. *paradoxa* and var. *neglecta* exceed in size and frequency of canals that of all other taxa including the closely related *E. atrorubens*.

The epidermal cells on the adaxial surface of the ligule offer characters of unusual interest even in the detection of hybrids and introgression. In one group of species the epidermal cells are uniform in shape, whether the outline is conical or bullet-shaped. In this group are *E. purpurea*, *E. laevigata*, *E. paradoxa* varieties, and *E. angustifolia* varieties. In other taxa the shapes are variable and the cells are relatively larger.

The population of plants produced as a result of introgression of *E. angustifolia* var. *strigosa*, *E. atrorubens* and *E. angustifolia* var. *angustifolia* have abaxial epidermal cells of two types. These consist of unicellular and multicellular hairs with the latter found in no other taxon of the genus. The multicellular hair consists of an enlarged basal cell with a neck and a catenuliform series of 1, 2, or 3 pyramidal cells.

After a comparative anatomical study was made, the following key based on a combination of stem, petiole, and ligule characters was developed. It distinguishes all taxa (except *tennesseensis*) nearly as well as a key based on morphology.

Resin canals present in both pith and cortex
- Stem with over 42 protoxylem points; resin canals originating opposite vascular bundles and interfascicular region
  - Resin canals present in ligule ..... *E. purpurea*
  - Resin canals absent in ligule ..... *E. laevigata*
- Stem with less than 42 protoxylem points; resin canals originating only opposite interfascicular region
  - Petiole with stone cells ..... *E. paradoxa* var. *neglecta*
  - Petioles without stone cells
    - Petioles with 3 air canals around median bundle and running length of the petiole ..... *E. atrorubens*
    - Petioles lacking air canals
      - Epidermis of stem with rectangular and straight walled cells ..... *E. paradoxa* var. *paradoxa*

Epidermis of stem with irregular walls; end walls oblique
Median vascular bundle of petiole fan-shaped .... *E. simulata*
Median vascular bundle round ..... *E. pallida*

Resin canals present only in cortex
Fibers absent in the pith ..... *E. sanguinea*
Fibers present throughout pith
Abaxial epidermal cells of ligule unicellular and multicellular
Introgressed population of *E. angustifolia* and *atrorubens*
Abaxial epidermal cells of ligule all unicellular
Epidermal cells of stem 27-57 μ long, mean 49 μ .....
E. angustifolia var. *strigosa*
Epidermal cells of stem 53-193 μ long, mean 115 μ .....
E. angustifolia var. *angustifolia*

CHROMOSOME NUMBERS

During this study chromosome numbers were obtained for all taxa except *Echinacea tennesseensis*. Over 2100 counts were made from buds fixed in the field, from the experimental garden, and the greenhouse. In many cases counts were obtained from root tips of germinated seed. As a result, chromosome counts were obtained from plants over most of the range of each taxon. A long list of documented counts could be given but appears to be superfluous. However, voucher specimens are deposited in the University of Kansas Herbarium.

Echinacea pallida consistently has n=22 as do most colonies of *E. angustifolia* var. *strigosa* in northern Texas and southern Oklahoma. All other taxa have n=11. In locations where *E. pallida* occurred with other species, a few triploid plants were found. These have been documented for natural hybrids of *E. pallida* and the following: *E. angustifolia* var. *strigosa*, *E. atrorubens*, *E. paradoxa* var. *paradoxa*, *E. purpurea*, and *E. simulata*. In one prairie in Douglas County, Kansas, a mixed colony of *E. pallida* and *E. atrorubens* consisted of 27% triploids.

Karyotypes of all species were determined from a study of mitotic metaphase chromosomes in seedling root tip cells. When the chromosomes of each species ideogram were arranged in the order of apparent comparable chromosomes, it became quite evident that all of the karyotypes are basically rather similar and of little aid in taxonomic decisions. It appears likely, however, that a very careful comparative study of karyotypes would be of use to a cytogeneticist in determining possible relationships.

TRANSPLANTS AND HYBRIDIZATION STUDIES

The period of time devoted to the study of *Echinacea* allowed for transplants to the experimental garden of all taxa except *E. tennesseensis*. The

smallest number of transplants obtained was 25 plants of *E. laevigata*, though over a hundred specimens of the latter were grown from seed. For all other taxa at least a hundred transplants were obtained. Except for *E. laevigata*, plants were obtained from over the range of the species.

In the common environment of the experimental garden, located on the west side of Lawrence, Kansas, a number of interesting observations were made. *E. sanguinea* plants from Texas and Louisiana failed to survive the Kansas winter in each of five years. Transplants of tetraploid *E. angustifolia* var. *strigosa* from Texas and southern Oklahoma also failed to survive though plants from diploid colonies of the variety flourished. Specimens of *E. laevigata* from Georgia survived for eight years and are still growing well with no sign of winter kill. Specimens of *E. angustifolia* var. *angustifolia* from western Oklahoma and Kansas average 60% mortality the first winter and have never survived more than two seasons.

Plants of *E. pallida* obtained at intervals from Texas to northwest Iowa exhibit a genetically fixed flowering time with plants from Texas flowering in early May and those from Iowa in early July. This flowering sequence exists as a cline as does the ligule color of white in the south to dark rose in the north. In the experimental garden the flowering dates are not as evident as in original habitat, but they are clearly observed. The ligule color does not vary from the color in the original habitat.

It was discovered early that plants of all taxa are self-sterile as proven by over 500 bagging experiments in both the experimental garden and greenhouse. As a result it was relatively easy to cross plants by simply bagging heads and later rubbing them together during each of three to five successive days.

In the crossing program over 5000 hybridizations were successfully completed, and all possible combinations (except for *E. tennesseensis*) were made. Voucher specimens of hybrids are in the University of Kansas Herbarium.

It was soon apparent that F_1 hybrids could be produced in all possible combination though percentage of success varied with the combination. The more morphologically dissimilar and geographically separated taxa were consistently the easiest to cross. Thus the cross between the short, strict, tuberculate-hirsute *E. angustifolia* var. *angustifolia* of western Kansas was always easy and successful with the tall, much branched, glabrous-stemmed *E. purpurea* of the eastern United States, and the F_1 regularly produced over 90% viable seed.

Attempts to cross the very closely related *E. simulata* and *E. sanguinea* proved most difficult and seldom produced over 10% viable seed. All crosses of *E. paradoxa* var. *paradoxa* with *E. a.* var. *neglecta* yielded 50% viable seed. It became apparent that ease of crossability reveals very little of tax-

onomic value in *Echinacea*. Attempts at producing backcrosses were relatively successful and progeny segregated much as would be expected. A detailed cytogenetic study would no doubt be interesting and reveal more on the lineage relationship of taxa, but I feel it would do little to aid in taxonomic decisions.

TAXONOMIC HISTORY

In *Species Plantarum* Linnaeus described an echinaceous plant under *Rudbeckia purpurea* and based this name on *Chrysanthemum americanum* of Plukenet (1720) and on *Dracunculus virginianus latifolius* of Morrison (1699). The illustration of Morrison is identical with what is now considered to be *Echinacea*. Necker (1790) described *Brauneria* but mentioned no species, and the description given is similar to that of *Rudbeckia*. Moench (1794) described the genus *Echinacea* and gave a good description of the generic characters. He based the genus on *Rudbeckia purpurea* L. which is the type species of *Echinacea*.

Echinacea was recognized by botanists until late in the nineteenth century. Alphonse DeCandolle (1836) recognized *Echinacea* and described four species. Nuttall (1834, 1841) described three species of which two are still valid. Torrey and Gray (1842) included three species in *Echinacea*. Gray, in editions of his Manual of Botany, recognized *Echinacea*. The seventh edition recognized *Brauneria* as did the first edition of *The Illustrated Flora of the Northern United States and Canada* by Britton and Brown (1898). Small (1903) reorganized *Brauneria* as have several authors since. The second and third editions of the *Illustrated Flora* and the eighth edition of *Gray's Manual of Botany* returned *Echinacea* as the valid name. The argument of whether *Brauneria* should be valid was settled at the ninth International Botanical Congress, in Montreal in 1959, when the nomenclature section voted in effect to consider the names of Necker's (1790) "species naturales" illegitimate as generic names. As the next oldest name, *Echinacea* becomes the valid name of the genus.

Beadle (1898) described *Brauneria tennesseensis* and Boynton and Beadle (1903) described *Brauneria laevigata*. Blake (1929) transferred *B. laevigata* to *Echinacea* and reduced *Brauneria tennesseensis* to a variety of *Echinacea angustifolia* DC. Small (1933) elevated *tennesseensis* as a species of *Echinacea*. Sharp (1935) in his "A Critical Study of Certain Epappose Genera—of the Compositae" recognized five species and one variety in *Echinacea*. He excluded one species, *Echinacea atrorubens* Nutt. and failed to properly evaluate the other species described by Nuttall (1841) as did Fernald (1900). Cronquist (1945) recognized three species and three varieties of *Echinacea*.

GENERIC DESCRIPTION

Echinacea Moench, Meth. Pl. 591. 1794.

Dracunculus Morrison, Pl. Hist. pt. 3, sec. 6, 42, pl. 9. 1699.
Bobartia Petiver, Herbal, 473. 1715. 1704.
Brauneria Necker, Elem. Bot. 1:17. 1790.
Helichroa Rof. Neogenyton, 3. 1825.

Herbaceous perennials, arising from vertical or horizontal rootstalks; stems erect, simple or branched, hirsute, hispid, strigose, or smooth and glaucous; leaves petiolate below, becoming sessile and reduced above, 3-5 veined, ovate, ovate-lanceolate, elliptical, entire or coarsely toothed, pubescent or smooth; heads singly terminating peduncuiform stem or branches; involucre conical or hemispherical; phyllaries in 3-4 series, imbricated, outer foliaceous, lanceolate to linear-lanceolate, attenuate, ciliate, smooth or pubescent, showing transition into pales; pales conduplicate, exceeding disk flowers, ending in sharp or blunt spines; ray-flowers sterile, in one series, ligules strap-shaped, bifid or trifid, rose-colored, purple, white or yellow, achenes trigonous; disk-flowers fertile, corolla expanded below into a fleshy bulblike base, sessile on ovary, tube cylindrical with 5-lobed erect limb; stamens 5, anthers sagittate at base, terminating into an ovate appendage; pollen yellow or white; achenes 4-angled, 3-5.5 mm long, pappus a smooth or toothed crown; chromosome number n=11, n=22. Type species: *Rudbeckia purpurea* L. Sp. Pl. 2:907. 1753.

KEY TO TAXA OF *ECHINACEA*

Leaves broadly to narrowly ovate, rounded at base, often serrate; pales with flexible tips
- Leaves smooth, glaucous, rarely strigose; pales with incurved tips ..... *E. laevigata*
- Leaves scabrous above, not glaucous; pales with straight tips ..... *E. purpurea*

Leaves lanceolate to linear lanceolate, attenuate to base, never serrate; pales with rigid tips.
- Stems and leaves strigose or strigose-hirsute
  - Ligules definitely longer than width of head
    - Ligules yellow; Ozarks of Mo. and Ark. ..... *E. paradoxa* var. *paradoxa*
    - Ligules purple, rose-colored, or white; Arbuckle Mt., Okla. ..... *E. paradoxa* var. *neglecta*
  - Ligules shorter to barely longer than width of head
    - Plant 5-10 dm tall; ligules dark red ..... *E. atrorubens*
    - Plant 2-5 dm tall; ligules pink or white ..... *E. angustifolia* var. *strigosa*
- Stems and leaves hirsute or hispid
  - Achenes 3 mm long; heads nearly hemispherical ..... *E. sanguinea*

Achenes 3.5-5 mm long; heads conical
Ligules 4-9 cm long, drooping.
Pollen white; West Ark., Mo., Tex. to N.W. Iowa .... *E. pallida*
Pollen yellow; Eastern Mo. & Ill. ..... *E. simulata*
Ligules 2-4 cm long, spreading
Stems and leaves softly hirsute;
Cedar Barrens of Tenn. ..... *E. tennesseensis*
Stems and leaves tuberculate-hirsute or hispid; High
Plains Tex. to Canada ..... *E. angustifolia* var. *angustifolia*

1. **Echinacea angustifolia** DC. var. **angustifolia.** Prodr. 5: 554. 1836.

Brauneria angustifolia Heller. Muhlenbergia 1: 5. 1900.
Echinacea pallida var. *angustifolia* (DC.) Cronq. Vasc. Pls. Pacif. Northw. 5: 160. 1955.

Stems simple or occasionally branched, 1-5 dm high, smooth or hirsute below, hirsute or tuberculate-hirsute to tuberculate-hispid above; leaves oblong-lanceolate to elliptical, entire, dark green, tuberculate-hirsute to tuberculate-hispid; basal leaves short to long-petiolate, 5-27 cm long, 1-4 cm broad, lower cauline leaves petiolate, 4-15 cm long, 0.5-3.8 cm broad, upper cauline leaves sessile, acute; heads 1.5-3 cm high, 1.5-2.5 cm broad exclusive of ligules, phyllaries in 3-4 series, lanceolate, acute, entire, 6-11 mm long, 2-3 mm wide, tuberculate-hirsute or tuberculate-hispid; rays spreading, 2-3.8 cm long, 5-8 mm wide, white, pinkish or purplish; disk-corollas 6-8.5 mm long, lobes 1.2-2 mm long; achenes 4-5 mm long, pappus a toothed crown; pollen grains yellow, 19-26 μ in dia. (ave. 22.5); chromosome number n=11.

DISTRIBUTION: Dry prairies and barrens. Minn. to Sask., south to Okla. and Texas. Fig. 1.

TYPE: Near Austin, Texas, *Berlandier 1692* (G, Photo!).

REPRESENTATIVE SPECIMENS EXAMINED: CANADA: MANITOBA: prairie, 1 mi w Ninette, 14 July 1953, *Askell* and *Doris Love* 6018 (US); near Brandon, 24 July 1896, *John Macoun 13927* (F,NY). SASKATCHEWAN: dry grassy slope, Estevan, 14 Aug. 1950, *Dore* and *Breitung 12568* (MO).

UNITED STATES: NORTH DAKOTA: Barnes Co.: prairie, Valley City, 10 July 1903, *Barber 152* (GH). Kidder Co.: sandy soil, 5 mi e Tappen, 15 July 1939, *Rollins* and *Munoz 2812* (GH, US). Williams Co.: rocky prairie, near Epping, 6 July 1930, *Palmer 36919* (MO, US). MONTANA: Custer Co.: gravelly hillsides, Miles City, 1 Aug. 1938, *Curfman GX21* (PH, OKL). Dawson Co.: 12 mi above Glendive, 15 July 1883, *Ward* (US). WYOMING: Converse Co.: near La Prele Reservoir, 6 Aug. 1942, *Porter 3154* (OKLA). Crook Co.: red beds, near Beulah, 3 Aug. 1926, *Hayward 221* (F, ILLS, US). COLORADO: Arapahoe Co.: vicinity Fort Logan, July 1935, *Cletus 64* (F). Los Animos Co.: rocky field, 1 mi ne Carrizo Mt., 6 July 1947, *Rogers 4657* (US). SOUTH DAKOTA: Aurora Co.: grassy bank, 9 mi w Aurora Center, 2 July 1960, *Harms 570* (KANU). Fall River Co.: roadside, 4 mi e Hot Springs, 6 July 1955, *Porter 6705* (TEX). Mellete Co.: 3 mi below White River, 1 July 1927, *Shantz 235* (ILL). Yankton Co.: rolling prairie, 12 mi n Yankton, *Richards 1304* (KANU). MINNESOTA: Big Stone Co.: virgin prairie, 2 mi n Ortonville, 24 June 1941, *Johnson 380* (ILL, GH, NY). Rock Co.: prairie, 1 mi e Luverne, 30 July 1958, *Richards 1292* (KANU). IOWA: Dickinson Co.: upland prairie, West Okoboji Lake, 11 Aug. 1916, *Shimek* (GH, MO, US). Emmet Co.: gravelly prairie, 4 mi nw Estherville, 16 July 1935, *Hayden 10691* (GA, US). Osceola Co.: prairie, 1 mi e 2 mi n, Allendorf, 31 July 1958, *Richards 1283* (KANU). NEBRASKA: Antelope Co.: prairie, 6.7 mi e Royal, 4 July 1960, *Harms 583* (KANU). Hamilton Co.: prairie, 14 mi w Aurora, 3 July 1958, *McGregor 13921* (KANU). KANSAS: Barber Co.: prairie, 6 mi nw Medicine Lodge, 18 June

FIG. 1. Distribution of *E. angustifolia* var. *angustifolia*, circles; *E. a.* var. *strigosa*, squares; *E. atrorubens*, triangles.

1957, *Lathrop 3815* (KANU). Cloud Co.: near Warren, 20 June 1883, *Carleton* (ILL). Ellis Co.: rocky outcrop, 2 mi w Hays, 8 July 1935, *Bondy 156* (DUKE, F, GH, MO, OKL, OKLA, TENN). Kiowa Co.: sandy prairie, 7 mi s Haviland, 12 June 1951, *McGregor 3736* (KANU, NY). Pottawatomie Co.: prairie meadow, 3 mi w Belvue, 15 June 1956, *Lathrop 2475* (KANU). OKLAHOMA: Beaver Co.: 6 mi e Forgan, 11 June 1948, *Waterfall 7865* (OKL, OKLA). Carter Co.: rocky prairie, 2 mi w Woodford, 17 June 1959, *McGregor 14327* (KANU). Woods Co.: prairie, near Cora, 18 May 1913, *Stevens 737* (MO, NY, OKL, OKLA). TEXAS: Armstrong Co.: gravelly hillside, 3.5 mi s Claude, 23 June 1945, *Shinners 8114* (SMU). Burnet Co.: Marble Falls, 28 May 1922, *Tharp 1346* (TEX, US). Gillespie Co.: open area, 4 mi n Fredericksburg, 16 June 1962, *Richards 3748* (KANU). Kerr Co.: near Kerrville, 7-14 May 1894, *Heller 1735* (GH, MO, NY, PH, US). Roberts Co.: rocky hillside, .2 mi sw Miami, 9 July 1948, *Richards 1101* (KANU).

In the high plains area of Texas, Oklahoma, Kansas, and north into Canada, *Echinacea angustifolia* DC. var. *angustifolia is* a well defined species characterized by its strict, low height, coarse tuberculate-hirsuteness, rays as long or shorter than width of disk, and the occurrence of sclerotic cells in the pith.

Eastward in Kansas, Nebraska, Iowa, Minnesota, and North Dakota, *E. a.* var. *angustifolia* progressively becomes taller, less tuberculate-hirsute, rays longer, and appears intermediate between *E. a.* var. *angustifolia* of the plains and *E. pallida* Nutt. Cronquist (1945) reduced *E. a.* var. *angustifolia* to a variety of *E. pallida* because of this apparent intermediate series which is very striking in herbarium specimens.

Several characters can be used to distinguish between *E. pallida* and the intermediate appearing series of *E. a.* var. *angustifolia*. *E. pallida* is a tetraploid (n=22), has white pollen, resin canals in both pith and cortex, lacks sclerotic cells in the pith, and the rays are distinctly longer than width of disk.

Transplants of *E. a.* var. *angustifolia* from the plains area and from the areas of intermediate forms were grown in the experimental garden which is about 40 miles east of the eastern distribution of the intermediates. During six years of study the transplants maintained their characteristics, indicating genetic control of characters involved. Numerous plants grown from seed obtained from the high plains plants consistently were nearly identical with their parents. Seed from the intermediate plants produced offspring exhibiting considerable variation but this variation occurs in nature though it decreases westward.

The explanation for the intermediate plants is due to hybridization of *E. a.* var. *angustifolia* DC. with *E. atrorubens* Nutt. in the Arbuckle Mountains and adjacent areas in Oklahoma. This has resulted in continued backcrossing of hybrids with *E. a.* var. *angustifolia* resulting in a nearly stable hybrid population in central Oklahoma, to be discussed later in connection with *E. angustifolia* DC. var. *strigosa* McGregor.

As a result of this hybridization, introgression of certain characters into *E. a.* var. *angustifolia* has occurred, forming the intermediate population of taller less hirsute plants with tendency toward longer rays. Other intro-

gressed characters are less fixed but are common enough to add to the variability of the intermediate colonies. In most colonies, therefore, plants occur with the dark red reflexed rays and nearly glabrous lower stem of *E. atrorubens*. The frequent branching of the plants is due to this hybrid influence as is the trend to longer rays. Introgression has not influenced the character of sclerotic cells in the pith. *E. angustifolia* is the only species in the genus with this character, and it occurs in all hybrids between *E. angustifolia* and other species.

Because of the extent of introgression, it is not possible to taxonomically distinguish between *E. a.* var. *angustifolia* of the plains and the intermediate population to the east as a nearly complete east-west cline exists.

2. **Echinacea angustifolia** DC. var. **strigosa** McGregor. Trans. Kans. Acad. Sci. 70:366-370. 1968.

Stems erect, frequently branched, often flexuous, glabrous below or nearly so, strigose or strigose-hirsute above, 3-6 dm high; basal leaves petiolate, 4-23 cm long, .4-1.3 cm wide, elliptical to lanceolate; cauline leaves petiolate below, sessile above, strigose or strigose-hirsute, often tuberculate hispid on or near the margins; peduncle 8-23 cm long; heads 1.5-2.8 cm high, 2.4-3.3 cm wide exclusive of rays; rays 2.3-3.1 cm long, 5-6 mm wide; phyllaries in 3-4 series, lanceolate, acute 6-11 mm long, hirsute, ciliate, passing into pales; pales 11-13 mm long, awn 2-3 mm long; disk corolla 6-8 mm long, lobes 1.5-2 mm long; achenes 4-5 mm long, pappus a toothed crown; pollen grains yellow, 19-23 μ in dia. (ave. 20.9); chromosome numbers n=11, n=22.

Distribution: Rocky prairies, gypsiferous soils. Cowley County, Kansas, central Oklahoma, and extreme north central Texas. Fig. 1.

Type: Oklahoma: Stephens Co.: 3 mi w Velma, open wooded sandy hillside, 7 June 1959, *McGregor 14329* (KANU!).

Representative specimens examined: Kansas: Cowley Co.: rocky bank, 2.1 mi n Arkansas City, 13 June 1960, *Harms 567* (KANU). Oklahoma: Blaine Co.: prairie w of Geary, 4 July 1928, *Myers 107* (OKL). Carter Co.: prairie, 2 mi w Fox, 7 June 1959, *McGregor 14328* (KANU). Cleveland Co.: open black-jack hills, 6 mi w Norman, 25 May 1936, *Demaree 12796* (MO, NY, OKL, PH, SMU, US). Payne Co.: rocky hill, 4 mi sw Stillwater, 26 May 1925, *Featherly* (NCU). Texas: Clay Co.: rocky prairie, 9 mi w Henrietta, 21 May 1961, *McGregor 16866* (KANU). Dallas Co.: grassy slope, 1.2 mi sw Lancaster, 3 June 1930, *Cory 57421* (SMU). Parker Co.: grassland and sand hills, 9 mi w Weatherford, 18 May 1947, *McVaugh 8360* (GH, SMU, TEX).

Variety *strigosa* is characterized as being short, frequently branched, stems somewhat flexuous, strigose to strigose-hirsute, lower stem green on drying and nearly glabrous.

In the area of the Arbuckle Mountains of Oklahoma, *E. a.* var. *angustifolia* and *E. atrorubens* have apparently hybridized, in the past, resulting in a large hybrid derived population here recognized as *E. a.* var. *strigosa*. *Echinacea atrorubens* is in contact with var. *strigosa* along the eastern distri-

bution of the latter while *E. a.* var. *angustifolia* is in contact to the west and north. *E. atrorubens* is found most frequently in heavy moist prairie soils and is thus ecologically somewhat isolated from var. *strigosa*. To the west var. *strigosa* blends imperceptibly into var. *angustifolia*. Most of the area occupied by var. *strigosa* is an intermediate climatic and physiographic region between the two parental species and one open for invasion. No other taxa of *Echinacea* are found in most of the area now occupied by var. *strigosa*.

A careful study of mass collections from many colonies of *E. a.* var. *strigosa* reveals very little variation within a colony. Eastern colonies are more uniform and characteristic, but colonies to the west merge with *E. a.* var. *angustifolia*. Thus it would appear that the hybrids have backcrossed with var. *angustifolia* as evidenced by the low height, preference for a drier habitat, constant occurrence of sclerotic cells of the pith, less reflexed and lighter colored ligules, and maintenance of some hirsute pubescence. Characters maintained from *E. atrorubens* consist of the nearly glabrous lower stem which tends to remain dark green on drying, strigose pubescence, and tendency toward some reflexing of ligules. The branching of var. *strigosa* is a character to be found in all hybrids between taxa of *Echinacea*.

In southern Oklahoma and northern Texas several colonies of var. *strigosa* have been found which are tetraploid (n=22). Field data indicate that colonies along the southern range of *strigosa* are all tetraploid. Eastern tetraploid colonies are characteristic of var. *strigosa* but the westernmost ones are distinguished from var. *angustifolia* primarily on the basis of their apparent hybrid characters.

Artificial F_1 hybrids produced from crossing *E. atrorubens* with *E. a.* var. *angustifolia* are very similar in morphology to *E. a.* var. *strigosa*. They are short, branched, have flexuous stems, strigose pubescence, lower stem glabrous and remaining green on drying. Pollen fertility is 80-90%, and the plants are more easily cultured than are either of the parents. The F_2 generation is produced easily and plants are vigorous. No meiotic irregularities are readily observed.

Naturally occurring hybrids are found between *E. atrorubens* and the "intermediate *E. a.* var. *angustifolia*" in a number of places from southern Kansas to the northern limit of the range of *E. atrorubens* in Shawnee County, Kansas. These plants are very similar to variety *strigosa*, but they are always rare. It appears evident that much of the character of the intermediate phase of var. *angustifolia* is the result of continued introgression. Thus the tendency to branch, for dark red rays, lower stem to be glabrous, and taller growth found in the intermediate *angustifolia* all the way to Minnesota and North Dakota would be explained.

Echinacea angustifolia var. *strigosa* appears to be a rather stable population except for the merging with var. *angustifolia* on the west. The future

status of var. *strigosa* is uncertain, but the tetraploid colonies forming the southern segment of the population indicate genetic isolation is taking place. A detailed cytological analysis will be given in a forthcoming paper.

3. **Echinacea atrorubens** Nutt. Trans. Am. Phil. Soc. n. ser. 7:354. 1841.

Rudbeckia atrorubens Nutt., Jour. Acad. Phila. 7:80. 1834.

Stems simple to rarely branched, 3-9 dm high, light-green, glabrous below to strigose or strigose-hirsute above; basal leaves petiolate, petiole 1-1.5 cm long, blade 4-15 cm long, 1-4 cm wide, upper leaves progressively smaller, petiolate to sessile, leaf blades oblong-lanceolate, lanceolate, elliptical or upper linear, strigose and ciliate; heads, 1.5-4 cm high, 2-3.6 cm broad; phyllaries in 3-4 series, narrowly lanceolate, attenuate, inner passing into pales, strigose, ciliate, abruptly reflexed; body of pales 7.2-9 mm long, awn 2-3 mm long; ligules dark purple, rarely pink or white, 1.9-3.3 cm long, 4-7 mm wide, shorter to as long as head, strongly reflexed; disk corolla tube 5.3-6.3 mm long, lobes 1.2-1.9 mm long; achenes 4-5 mm (ave. 4.2) long, glabrous, grey, stramineous or brown, teeth or pappus crown unequal in length, longest tooth 1-3 mm; pollen grains 21-23 μ in dia. (ave. 21.3); chromosome number n=11.

Distribution: Prairies, in a narrow band from Houston, Texas, to Ardmore, Oklahoma, and Topeka, Kansas. Fig. 1.

Type: Plains of *Arkansas: Nuttall* (PH !).

Representative specimens examined: Kansas: Anderson Co.: prairie, 5 mi se Garnett, 10 June 1959, *McGregor 14366* (KANU). Cowley Co.: rocky prairie, 4 mi n Cambridge, 9 June 1955, *McGregor 10396* (KANU). Lyon Co.: roadside, 5.5 mi s Emporia, 11 June 1960, *Harms 337* (KANU). Oklahoma: Choctaw Co.: prairie, 1 mi n Forney, 20 May 1961, *McGregor 16848* (KANU). Major Co.: gypsum exposure, Glass Mt., near Togo, 1 May 1936, *Demaree 12367* (MO, NY, OKL). McCurtain Co.: prairies, near Idabel, 18 May, 1916, *Houghton 3642* (GH, MO, NY). Roger Mills Co.: red sandstone, 11 mi s Cheyenne, 15 June 1948, *Waterfall 7068* (OKL, OKLA). Texas: Cooke Co.: Roadside bank, 14 mi e Gainesville, 21 May 1961, *McGregor 16861* (KANU). Polk Co.: open woods, near Livingston, 23 May 1917, *Palmer 12015* (GH, NY, US). Tarrant Co.: dry sterile ground, no loc., 8 June 1924, *Ruth 243* (GH, MO, NY, PH, SMU, US).

Echinacea atrorubens Nutt. is a well defined species at once separated from other taxa of the genus by its dark purple ligules, 1.9-3.3 cm long, and so sharply reflexed that the tips of the ligules curve in and often contact the stem just below the head. Plants are tall with light green stems which are nearly glabrous below to strigose or rarely strigose-hirsute above. These characters and its distribution readily separate *E. atrorubens* from *E. paradoxa* var. *paradoxa* and *E. p.* var. *neglecta* with which it long has been confused as noted below.

Nuttall (1834) described *Rudbeckia atrorubens* and later (1841) transferred the species to *Echinacea*. His description was brief but good, and it along with the type specimen clearly represents a species of *Echinacea*.

Torrey and Gray (1842) described a true *Rudbeckia* as a variety of *E. atrorubens* Nutt. and gave the name *E. a.* var. *graminifolia*. Later, Chapman (1860) interpreted the supposed variety as the plant first described by Nuttall as *Rudbeckia atrorubens* and transferred it as *Echinacea atrorubens* Chap. This error was further complicated by Gray (1886) who abandoned the first name supplied to the true *Rudbeckia* and adopted the earlier name of Nuttall so that the name *Rudbeckia atrorubens* Gray appears in his Synoptical Flora.

Boynton and Beadle (1901) clearly recognized these errors and correctly interpreted Nuttall's *Echinacea atrorubens* as a valid species though they transferred it to *Brauneria*. They recognized the variety *E. a.* var. *graminifolia* as a true *Rudbeckia* and made the combination *R. graminifolia* (T. & G.) Boynton and Beadle.

In their treatment of *Brauneria* in Small's *Flora of the Southeastern United States*, Boynton and Beadle (1903) proceeded to confuse the understanding of the species which they had clarified two years before. Norton (1902) had described *Brauneria paradoxa*, and in Small's Flora, Boynton and Beadle apparently included *B. paradoxa* in their description of *B. atrorubens* by broadening the description to cover both, although no synonomy was given. They gave its distribution as Arkansas and Missouri.

Robinson and Fernald (1908), in the 7th edition of Gray's Manual, recognized *Brauneria paradoxa* Norton and listed "?*B. atrorubens* Britton, in part, not Nutt.", as a synonym. Their description is that of *B. paradoxa* (rays bright yellow). Distribution was given as Missouri to Texas. The whole significance of *Echinacea atrorubens* Nutt. was therefore lost.

Sharp (1935), in his treatment of *Echinacea*, excluded *Echinacea atrorubens* Nutt. from the genus apparently on the basis of the interpretation of Gray (1886) that *Rudbeckia atrorubens* Nutt. was truly a *Rudbeckia*. Palmer (1936) came close to correcting matters as he recognized *Brauneria atrorubens* as a valid name, but specimens from Platt National Park in Oklahoma seemed so close to *B. paradoxa* with which he was familiar that he hesitated to make a taxonomic decision. The Oklahoma plants which puzzled Palmer are recognized by me as a variety of *E. paradoxa* endemic in the Arbuckle Mountains of Oklahoma. Palmer (l.c.) was comparing *E. paradoxa* var. *paradoxa* with *E. paradoxa* var. *neglecta*. Thus he was unable to define *E. atrorubens* in a satisfactory way.

Cronquist (1945) was the last to misinterpret the taxa under discussion, primarily because very few specimens of *E. atrorubens* had been collected by botanists. Thus he compared the same material as Palmer with the result that he reduced *paradoxa* to a variety of *E. atrorubens*.

Some of the confusion in the range of *E. atrorubens* has been due to Nuttall's statement of its occurrence on the "plains of Arkansas." This has

been interpreted as the state of Arkansas. It appears more possible that Nuttall meant plains of the Arkansas River and that he actually collected the specimen in Oklahoma as he was in the area of Oklahoma where *E. atrorubens* still occurs.

4. **Echinacea laevigata** (Boynton & Beadle) Blake. Journ. Wash. Acad. Sci. 19:273. 1929.

Brauneria laevigata Boynton & Beadle in Small, Fl. Southeast U.S. ed. 1, 1261. 1903.
Echinacea purpurea var. *laevigata* Cronq. Rhodora 47:397. 1945.

Stems erect, rarely branched, glabrous, glaucous, 5.5-10 dm high; basal leaves long petiolate, petioles 0.8-2 dm long, blade 0.8-1.6 dm long, 2-6.5 cm broad, blades tapering to base, elliptical to broadly lanceolate, glabrous to rarely minutely strigose above or slightly hirsute, glaucous, lower cauline petiolate to sessile above, similar to basal; peduncle 1.1-3.4 dm long; heads 1.5-2.5 cm high, 1.5-3.4 cm broad; phyllaries in 3-4 series, lanceolate 9-12 mm long, glabrous, often ciliate, passing into the pales; pales 10-12 mm long, awn 2.5-3.5 mm long, often incurved; disk flower corolla 8-9 mm long, lobes 1.5-2 mm long; rays 3.5-8 cm long, 5-6 mm wide, purplish or light pink; achenes 4-5 mm long, pappus a crown of equal teeth; pollen grains yellow, 19-21 μ in dia. (ave. 19.5); chromosome number n=11.

Distribution: Open woods, and fields. Pennsylvania, Virginia, south to mountains of Georgia. Fig. 2.

Type: South Carolina: Near Seneca, June 1888. *Gerald McCarthy* (US !).

Representative specimens examined: Georgia: Stephens Co.: mountain slopes, 1 mi n Currahee Mt., 29 June 1950, *Duncan 11209* (GA, GH, MO, SMU). North Carolina: clearing of beech-black-jack oak woodland, near Eno River, 18 June 1951, *Godfrey* and *Fox 51165* (GH, MO, SMU, TENN). Orange Co.: woods, 2 mi e Chapel Hill, 12 June 1928, *Coker* (NCU). South Carolina: Aconee Co.: vicinity of Seneca, June 1888 *McCarthy* (US); near Keowee, 22 May 1906, *House 2206* (MO). Pennsylvania: Lancaster Co.: Caernsvron township, July, coll. unknown (MO). Virginia: Bedford Co.: no loc., July *Curtiss 1420* (KANU). Campbell Co.: railway bank, Lynchburg, 1 July 1929, *Murrill* (NY). Montgomery Co.: opening in mixed woods, 2.5 mi w Shawsville, 27 June 1938, *Massey 2015* (GH). Roanoke Co.: exposed shale barren, 2.9 mi n Dixie Caverns, 13 July 1942, *Wood 3921* (GH). Wythe Co.: wet meadows Wytheville, 1874, *Shriver* (PH); near Stanton, 18 June 1896, *Murrill* (NY).

This species was described by Boynton and Beadle(1903) as *Brauneria laevigata* and was separated from other taxa by awn of pales shorter than body; plant glabrous or glabrate; and leaf-blades lanceolate to oblanceolate. Blake (1929) transferred the species to *Echinacea* and reported it as still known only from the original specimens. Sharp (1935) recognized *laevigata* but utilized only the smooth and glaucous character of stem and leaves to separate it from *E. purpurea*. Cronquist (1945) reduced *laevigata* to a variety of *E. purpurea* because a specimen was found "to have upper surface of the leaves short hirsute, but otherwise glabrous." None of these workers had

FIG. 2. Distribution of *E. purpurea*, circles, and *E. laevigata*, squares.

more than four collections on which to base their decisions. Fernald (1950) listed incurved tips of pales as a character of *laevigata*.

E. laevigata is a clearly defined species but closely related to *E. purpurea*. It differs from the latter in having a vertical caudex and tap-root; strict, rarely branched, glabrous and glaucous stem; leaf blades broadly lanceolate to elliptical; glabrous to rarely minutely strigose or hirsute, glaucous; rays longer and more slender; and awn of pales one-fourth of the length of the body and somewhat incurved.

Artificial hybrids produced between *laevigata* and *purpurea* have a high degree of pollen sterility (70-80%) and are in general weak and fail to survive.

5. **Echinacea pallida** (Nutt.) Nutt. Trans. Am. Phil. Soc. II. 7:354. 1841.

Echinacea angustifolia Hook. Curt. Bot. Mag. 17: pl. 5281. 1861. non DC.
Rudbeckia pallida Nutt. Journ. Acad. Sci. Phil. 7:17. 1834.
Brauneria pallida Britt. Mem. Torr. Bot. Club. 5:333. 1894.
Echinacea pallida f. *albida* Steyerm. Rhodora 44:150. 1942.

Stems simple, rarely branched, 4-9 dm high, sparsely hirsute below, more densely so above; leaves oblong-lanceolate to long-elliptical, entire, dark green, hirsute on both surfaces, triple-veined; basal leaves 1-3.5 dm long, 1-4 cm broad, the cauline 1-2.5 dm long, 1-2.5 cm broad, acute, petiolate below to sessile above; phyllaries lanceolate to narrowly oblong, 8-17 mm long, 2-4 mm broad, hirsute, ciliate, 3-4 series, gradually passing into the echinaceous pales; rays reflexed, 4-9 cm long, 5-8 mm broad, purplish, pink, or white; pales 10-13 mm long, body 8-10 mm long, awn 2.5-3.5 mm long; disk floret 8-10 mm long, lobes2 -3 mm long; achenes 3.7-5 mm long, glabrous, pappus a toothed crown, teeth about even, longest 1 mm; pollen grains white, 24-28.5 μ in dia. (ave. 26.1); chromosome number n=22.

DISTRIBUTION: Rocky prairies, open wooded hillsides, and glades. Northern Indiana and Illinois, Iowa, western Missouri, Arkansas, northeastern Texas north to Nebraska. Introduced and adventive eastward. Fig. 3.

TYPE: Arkansas Territory: 1819, *Nuttall* (BM, Photo !).

REPRESENTATIVE SPECIMENS EXAMINED: ALABAMA: Green Co.: roadside bank, Entaw, 14 May 1955, *Sargent 7165* (SMU). ARKANSAS: Ashley Co.: low ridges, Hamburg, 25 June 1939, *Demaree 19377* (SMU). Benton Co.: rocky hillside, 5 mi e Springdale, 11 June 1958, *McGregor 13890* (KANU). Drew Co.: prairie, Ladelle, 6 May 1939, *Demaree 19124* (GH, NY, OKLA, SMU, TENN). GEORGIA: Bartow Co.: open pine-deciduous woods, .75 mi sw Allatoona Dam, 5 June 1948, *Duncan 8248* (GA, GH, MO). Floyd Co.: moist soil, near locks on Coosa River below Rome, 5 Aug. 1912, *Pennell 4087* (NY). ILLINOIS: Adams Co.: along railroad, ne Quincy, 21 June 1943, *Evers, Jones* and *Jones, 1158* (ILL, NY). Jersey Co.: near Grafton, 13 July 1958, *Jones 22181* (ILL). Peoria Co.: original prairie, Horse Shoe Bottom, June 1951, *Chase 12024* (OKL, TEX). INDIANA: Benton Co.: dry prairie roadside, 6 mi s Free, 30 Aug. 1916, *Deam 21546* (GH). IOWA: Boone Co.: Prairie Ledges State Park, 30 June 1926, *Pammel 243* (MO, NY, US). Jasper Co.: prairie, 3 mi e Newton, 6 July 1956, *Van Bruggen 589* (US). KANSAS: Anderson Co.: prairie, 2 mi e Welda, 5 June 1956, *McGregor 12320* (KANU). Butler Co.: rocky prairie, 3.8 mi s Leon, 13 June 1960, *Harms 357* (KANU). Leavenworth Co.: prairie, 5 mi sw Tonganoxie, 15 June 1956, *Lathrop 2467* (KANU). MICHIGAN: Baraga Co.: old fields, no loc., July 1885, Farwell (DUKE). Charlevoix Co.: sandy ground between woods and road, Beaver Island, 25 July 1957, *Voss 4756* (SMU). MISSOURI: Barry Co.: rocky bank, 7 mi ne Seligman, 11 June 1958, *McGregor 13875* (KANU). Cole Co.: limestone glade over bluffs, 4 mi n St. Thomas, 18 Aug. 1937, *Steyermark 24958* (F, MO). Jasper Co.: along railroad, 1.8 n Carthage, 1 June 1960, *Harms 310* (KANU). Stone Co.: high bluffs, Galena, 28 May 1914, *Palmer 5783* (MO, US). NEW YORK: Oswego Co.: near Oswego, 29 June 1887, *Stewart* (US). NORTH CAROLINA: Gaston Co.: roadside, 1.7 mi s Bessmer City, 26 July 1959, *Horton 1588* (NCU). McDowell Co.: cleared upland woods, 4.3 mi n McDowell-Rutherford Co. line on US 221, 1 September 1956, *Ahles 17801* (NCU). OKLAHOMA: Adair Co.: rocky bank, 2 mi n Chewey, 10 June 1959, *McGregor 14350* (KANU). Cherokee Co.: prairie, 3 mi w Tahlequah, 18 June 1951, *Waterfall 10044* (OKL, OKLA, SMU, TEX, US). Choctaw Co.: prairie, near Hugo, 15 May 1936, *Demaree 12590* (MO, NY, OKL, PH, SMU). Pittsburg Co.: prairie, 5 mi w McAlester, 13 June 1958, *McGregor 13895* (KANU). TENNESSEE: Rutherford Co.: prairie, 6 mi sc Murfreesboro, 30 June 1957, *Deselm 1603* (TENN). TEXAS: Bowie Co.: prairies, near Buchanan, 13 June 1898, *Eggert* (MO). Fannin Co.: prairie, 1 mi w Windom, 21 May 1960, *McGregor 16860* (KANU). Red River Co.: near Bogata, 19 June 1917, *Tharp 47399* (TEX). VIRGINIA: Frederick Co.: roadside bank, west of Middletown, 1 July 1933, *Griscom* and *Hunnewell 18761* (GH). WISCONSIN: Dane Co.: near Madison, 1860, *Jackson* and *Watson* (PH). Rock Co.: prairie relic, 4 mi sw Clinton, 22 June 1941, *Wadmond, Shinners, Stearns* (F, NY).

Nuttall (1934) described *Rudbeckia pallida*, from specimens collected by him and Dr. Pitcher in Arkansas, as "resembling *R. purpurea* except that it had long petiolated narrow and almost perfectly entire leaves and rays pale

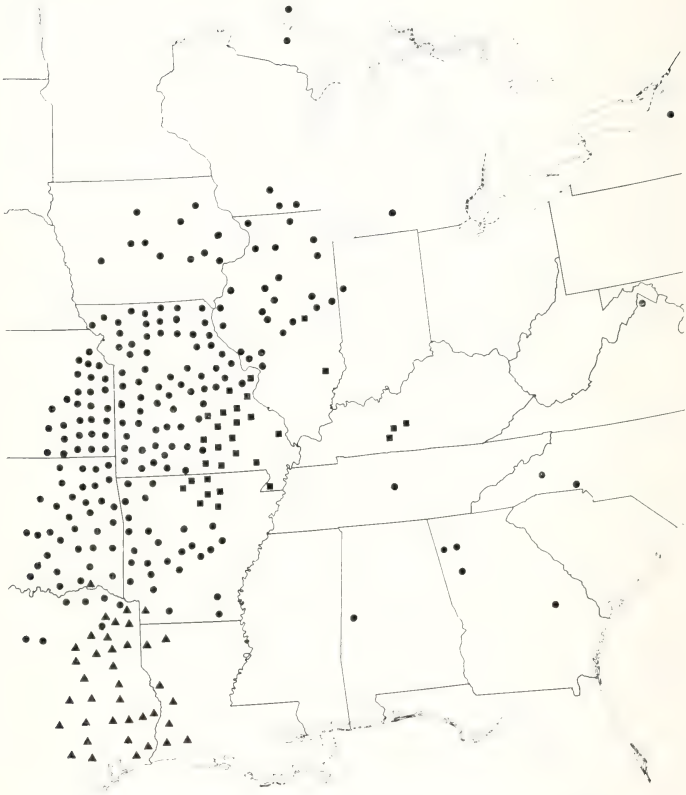

FIG. 3. Distribution of *E. pallida*, circles; *E. sanguinea*, triangles, and *E. simulata*, squares.

purple or almost rose red." Later Nuttal (1841) transferred the species to *Echinacea* with the added note that flowers were pale rose to almost white. Botanists have long recognized *E. pallida* and *E. purpurea* as the two valid, stable members of the genus.

Echinacea pallida is an apparent segmental allotetraploid and was probably derived from a hybrid between *E. simulata* and *E. sanguinea* followed by doubling of chromosome number. *Echinacea sanguinea* ranges north to southeast Oklahoma and southwest Arkansas. *Echinacea simulata* extends from eastern Missouri southwest to north central Arkansas. Thus the two

parents are now separated by about 200 miles. I presume that the two species hybridized somewhere in central Arkansas to northeast Texas, and after developing the polyploid condition, *E. pallida* migrated west along the Red and Arkansas Rivers and then northward.

On the ridges and slopes of the Fourche Mountains west of Little Rock, Arkansas, the Arkansas River Valley and southern slopes of the Boston Mountains west to Oklahoma, *Echinacea pallida* consists of a race characterized by smaller heads, narrower leaves, more slender and somewhat shorter stems, and often a tendency toward hemispheric heads. This race has a geographic range and could be recognized as a weak taxonomic variety. Many features of this race are similar to a combination of characters of *E. simulata* and *E. sanguinea* though its tetraploid condition, white pollen, and other characters identify it with *E. pallida*. West toward Oklahoma these *simulata* and *sanguinea* characters diminish until characteristic *pallida* is found in Oklahoma.

Between the Arkansas and Red Rivers and west of the Ouachita Mountains in Oklahoma, *E. pallida* has light pale rose to white ligules. Large colonies often are entirely white or white with a few pale rose plants. North to Kansas, Missouri and Iowa the rose color deepens in expression, pure white disappears, and dark rose red dominates. Thus a color cline from south to north occurs as does a progressively more sturdy stem and wider leaf.

Artificial F_1 hybrids between *E. simulata* and *E. sanguinea* appear very similar to the Arkansas race of *E. pallida*. The hybrids are fertile (85-90% of pollen) and back crosses have been grown. This work was handicapped because *E. sanguinea* is not winter hardy in Kansas, and though the hybrids are more hardy, a high rate of winter kill always results.

The use of this species as a drug plant no doubt is responsible for its introduction and scattered distribution throughout the eastern part of North America.

6. **Echinacea paradoxa** (Norton) Britton var. **paradoxa,** Ill. Fl. ed. 3:476, Fig. 4459. 1913.

Brauneria paradoxa Norton. Trans. Acad. Sci. St. Louis 12:40. 1902.
E. atrorubens Nutt. var. *paradoxa* (Norton) Cronquist. Rhodora 47(564): 396-403. 1945.

Stems simple, 3.5-8.5 dm high, stramineous or yellowish-green, sparsely or very rarely densely strigose; leaves oblong-lanceolate to long elliptical, entire, light green, 3-5 veined, strigose pubescent on both surfaces, more densely so below, margins scabrous ciliate; basal leaves petiolate, petiole 0.2-1.2 dm long, blade 0.5-2.3 dm long, 0.5-4 cm broad, the cauline 0.3-2 dm long, 0.5-2.5 cm broad, petiolate below, sessile above, acute; involucral bracts in 3-4 series, 7-12 mm long, 1-4 mm broad, lanceolate to ovate-lanceolate, acute

to attenuate, the outer foliaceous, the inner passing into pales, strigose or glabrous, ciliate; rays 3-7 cm long, 5-8 mm broad, lanceolate or narrowly oblanceolate, yellow; pales 10-13 mm long, body 9-11 mm long, awn 2-3.2 mm long; disk corolla 4-5 mm long, lobes 2 mm long; achenes 4.5-5.5 mm (ave. 4.8) high, glabrous, teeth of pappus crown nearly equal in length; pollen grains 21-25 μ in dia. (ave. 23.6); chromosome number n=11.

DISTRIBUTION: Rocky prairies, glades and bald knobs. Central and western Ozark region of Missouri and north-central Arkansas. Fig. 4.

TYPE: MISSOURI: Taney Co.: Swan, common "Big Baldy," 10 June 1898, *B. F. Bush 155* (Holotype MO!; isotypes at MO!, NY!, OKL!, GH!).

REPRESENTATIVE SPECIMENS EXAMINED: ARKANSAS: Baxter Co.: in glades, east of Mt. Home, 9 June 1933, *Moore 330162* (UARK). MISSOURI: Barry Co.: common in barrens, Eagle Rock, 4 June 1897, *Bush 76* (GH, MO, NY, US). Benton Co.: rocky prairies, near Lincoln, 23 June 1930, *Palmer 36760* (GH, US). Phelps Co.: rocky open hillside, .5 mi n Rolla, 8 June 1960, *McGregor 15644* (KANU). Wright Co.: limestone glade, 2 mi se Cedar Gap, 28 July 1937, *Steyermark 23731* (F, MO, NY, TENN).

Echinacea paradoxa var. *paradoxa* differs from all other members of the genus in having bright yellow rays and by being endemic to the west-central and southern Ozarks of Missouri and north Arkansas. In drying, both var. *paradoxa* and var. *neglecta* become distinctively brownish or stramineous.

Natural hybrids between var. *paradoxa* and *E. simulata* have been found where the two grow together. These are essentially seed sterile but do backcross naturally to var. *paradoxa*. No indication of backcrossing to *simulata* has been observed. The ligules of hybrids are mottled orange-red and continued backcrossing to var. *paradoxa* results in a lemon-yellow ligule with reddish base. Some plants of var. *paradoxa* with bright yellow ligule and a red spot at the base have reduced pollen fertility (70%) and are no doubt hybrid derivatives. Sterile triploid hybrids between var. *paradoxa* and *E. pallida* have been found. These are always similar to var. *paradoxa* except for mottled ligule color, increased pubescence, and greener stem and leaves. Artificially produced hybrids are similar to those found in nature.

7. **Echinacea paradoxa** (Norton) Britton var. **neglecta** McGregor. Trans. Kans. Acad. Sci. 70:366-370. 1968.

Stems simple, 3-8 dm high stramineous or yellowish-green, sparsely to densely strigose, sometimes lightly hirsute below head; leaves oblong-lanceolate to long-elliptical, the upper linear-lanceolate, entire, light green, 3-to rarely 5-nerved, strigose-pubescent on both surfaces, more densely so below, margins scabrous-ciliate; lower leaves with petioles 0.2-1.3 dm long, blade 0.4-2.5 cm wide, upper leaves becoming sessile; involucral bracts in 3-4 series, 7-12 mm long, 1-3 mm wide, lanceolate to ovate-lanceolate, acute to attenuate, the outer foliaceous, the inner passing into pales, strigose or glabrous, ciliate, rays 3-7 cm long, 5-8 mm wide, narrowly oblanceolate to lanceolate, light

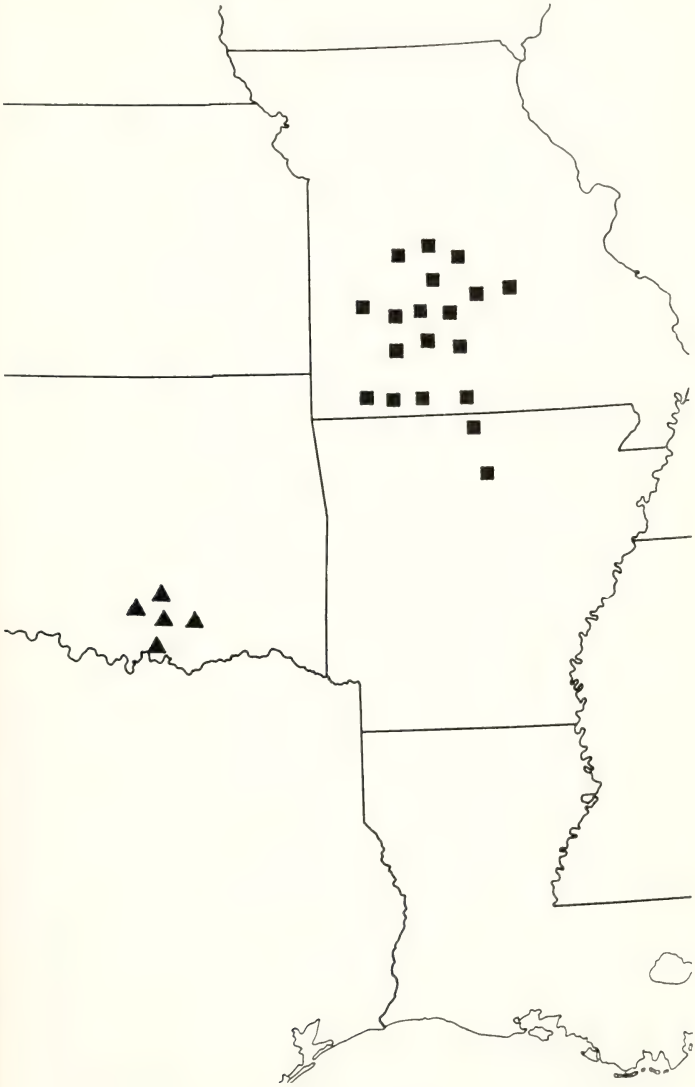

FIG. 4. Distribution of *E. paradoxa* var. *paradoxa*, squares, and *E. p.* var. *neglecta*, triangles.

purple, pink or white; pales 11-14 mm long, body 9-11 mm long, awn 2-3 mm long; disk corolla 4-5 mm long, lobes 2-3 mm long; achenes 4.5-5.5 mm (ave. 4.9) high, glabrous, teeth of pappus crown nearly equal in length; pollen grains 24-27 μ in dia. (ave. 26); chromosome number n=11.

DISTRIBUTION: Rocky prairies and open wooded hillsides. Arbuckle Mountain area of Oklahoma. Fig. 4.

TYPE: OKLAHOMA: Murray Co.: Platt National Park, 7 June 1959, *R. L. McGregor 14324* (KANU!).

REPRESENTATIVE SPECIMENS EXAMINED: OKLAHOMA: Atoka Co.: open slopes, 3 mi ne Atoka, 8 June 1947, *Robbins 2570* (OKL). Johnston Co.: open wooded hillside, Water Tower Hill, Tishomingo, 19 June 1951, *Cory 58896* (OKLA, SMU). Marshall Co.: prairie, 3.6 mi e Kingston, 7 June 1958, *Richards 546* (KANU). Murray Co.: rocky prairie, 1 mi s Sulphur, 29 May 1960, *McGregor 15606* (KANU). Pontotoc Co.: along railroad, 3 mi se of Ada, 26 May 1951, *McCoy 639* (OKLA). TEXAS: no loc., Flora Texana exsiccata Fasc. 1.94., 1843, *Lindheimer, F.* (SMU).

Var. *neglecta* is readily distinguished from var. *paradoxa* by its rose-colored, purple, or white ligules and by its geographic distribution. It has been determined previously by collectors as *E. pallida, E. atrorubens, E. angustifolia* and *E. paradoxa*. Failure to recognize the plant as an entity has been responsible for the confusion concerning *E. atrorubens*. This problem is discussed in connection with the latter species.

8. **Echinacea purpurea** (L.) Moench. Meth. Pl. 591. 1794.

Rudbeckia purpurea L. Sp. Pl. 2: 907. 1753.
Rudbeckia hispida Hoffmgg. Verz. Pfl. Nacktr. 1. 223.
Echinacea purpurea var. *arkansana* Steyermark. Rhodora 40:71. 1938.
Echinacea purpurea, f. *Liggettii* Steyerm. Rhodora 44:150. 1942.
Rudbeckia serotina Sweet. Brit. Fl. Gard. 1: pl. 4. 1823-25.
Echinacea speciosa Paxt. Mag. Bot. 15:79. 1849.
Echinacea intermedia Lindl. in Paxt. Mag. Bot. 15:79. 1849.
Brauneria purpurea (L.) Britt. Mem. Torr. Bot. Club 5:334. 1893.

Stems erect, stout, branched, hirsute or glabrous, 6-18 dm high; basal leaves ovate to ovate-lanceolate, acute, coarsely or sharply serrate, petioles up to 2.5 dm long, blades to 2 dm long and 1.5 dm wide, blade abruptly narrowing to base, often cordate, decurrent on petiole, 3-5 veined; cauline leaves petiolate below, sessile above, 7-20 cm long, 1.5-8 cm broad, coarsely serrate to entire, rough to the touch on both surfaces; phyllaries linear-lanceolate, attenuate, entire, pubescent on outer surface, ciliate, passing into the chaff; heads 1.5-3 cm long, 5-10 mm broad, purplish; pales 9-13 mm long, awn half as long as body; disk corollas 4.5-5.5 mm long, lobes 1 mm long; achene 4-4.5 mm long, pappus a low crown of equal teeth; pollen grains yellow, 19-21 μ in dia. (ave. 20.4); chromosome number n=11.

DISTRIBUTION: rocky open woods, thickets, and prairie. Georgia to La. and eastern Oklahoma, north to Ohio, Michigan, Illinois, and Iowa; adv. northeastward. Fig. 2.

TYPE: In Virginia, Carolina (LINN, Photo!).

REPRESENTATIVE SPECIMENS EXAMINED: ALABAMA: Franklin Co.: near Russellville, Sept. 1942, *James 43* (MO). Talladega Co.: near Sylacauga, 17-19 July 1900, *Pollard* and *Mason 216* (GH, NY, US). ARKANSAS: Benton Co.: rocky open woods, near Hiwassie, 3 Aug. 1933, *Palmer 42082* (GH, MO, NY, US). Izard Co.: open wooded hillside, 1 mi nw Calico Rock, 7 Aug. 1959, *McGregor 14977* (KANU). Logan Co.: rocky ridges, Magazine Mt., 18 June 1938, *Demaree 17742* (GH, NY, OKLA, SMU). Montgomery Co.: oak-hickory woodland, 5 mi n Collier Spring, 24 June 1967, *Janet Bare 199* (KANU). GEORGIA: Bartow Co.: roadside bank, .2 mi w Little Pinelog, 21 July 1948, Duncan 8590 (GA, GH, MO, TENN). Randolph Co.: dry rocky woods, near Griers Cave, 17 July 1903, *Harper 1884* (GH, F, MO, NY, US). ILLINOIS: Clay Co.: prairie strip, nw corner of county, 12 Aug. 1950, *Ahles 2888* (ILL). Stark Co.: near Wady Petra, 19 July 1900, *Chase 685* (F, GH, MO, PH). INDIANA: Cass Co.: sandy low prairie patches, .5 mi e Lake Cicott, 26 Sept. 1936, *Friesner 19140* (DUKE, F, GA, ILL, NY, OKLA, SMU). KENTUCKY: Carter Co.: moist open woods, Cascade Caverns, 17 July 1940, *Gilbert 872* (DUKE, GH, NY, OKL, PH, TENN, US). MISSOURI: Adair Co.: open woods, 4 mi n Kirksville, 3 July 1933, *Palmer & Steyermark 41176* (MO). Howell Co.: wooded hillside, 5 mi w Pomona, 8 Aug. 1959, *McGregor 14978* (KANU). MISSISSIPPI: Copiah Co.: shady woodland, no. loc., 7 Sept. 1942, *Moldenke 13881* (OKLA, SMU). NEW YORK: Albany Co.: spreading from cultivation, near Loudonville, 24 Aug. 1944, *House 29622* (GA). NORTH CAROLINA: Buncombe Co.: open woods, near Biltmore, 22 June 1897, *Chase* (F). Burke Co.: oak-maple woods, on NC26, 18 Aug. 1949, *Radford 4895* (NCU). OHIO: Adams Co.: prairie, no loc., 5 Oct. 1930, *Stephenson* (MO). Highland Co.: limestone soil, Brush Twp., 15 July 1937, *Bartley & Pontius 562* (NY). OKLAHOMA: Adair Co.: wooded valley, 3 mi s Kansas, 7 July 1950, *Waterfall* (OKLA, SMU, TEX). Delaware Co.: wooded valley, 24 mi e Tahlequah, 14 June 1958, *Wallis 7390* (KANU, OKLA, SMU, TEX). McCurtain Co.: prairie along railroad, 3 mi w Garvin, 20 May 1961, *McGregor, 16853* (KANU). TENNESSEE: Anderson Co.: roadside near Norris, 24 July 1934, *Sharp 2757* (GA). Dickson Co.: open thicket, 1 mi w Tennessee City, 13 June 1962, *McGregor 17172* (KANU). TEXAS: Bowie Co.: open woods, 2 mi n Texarkana, 12 July 1965, *Correll 31258* (ILL). VIRGINIA: Bedford Co.: no loc., 18 July 1871, *Curtiss* (GH).

Echinacea purpurea is the most widespread but not the most abundant species in the genus. It is very distinct and readily recognized by its tall branching habit; awns of pales as long as body; lower leaves ovate and often toothed; and its dull purple ligules. In Missouri, Arkansas, and Oklahoma the stems of *purpurea* are hirsute but east of the Mississippi River single plants and often entire colonies are found with smooth and somewhat glaucous stems. However, all degrees of hirsute to glabrous stems are frequently found in the same colony. As no geographic patterns can be determined, it appears any taxonomic recognition is unwarranted. A number of ligule color variants are found throughout the range of the species and may be of horticultural interest though taxonomically insignificant.

The variety *arkansana* Steyermark is an early season form found in relatively open areas of southeast Oklahoma, northeast Texas and adjacent Arkansas. It is smaller than *purpurea* in all respects, much less branched, and blooms in May and June. However, transplants of typical *E. purpurea* from the Missouri Ozarks into the open experimental garden developed into an early-blooming phase identical to var. *arkansana*. Plants of *arkansana* transplanted into a wooded area were identical with *purpurea* in habit and flowering time. Thus the variety has no taxonomic validity.

9. **Echinacea simulata** McGregor. Sida 3:282. 1968.

Echinacea speciosa McGregor. Trans. Kans. Acad. Sci. 70:336-370. 1968.

Stems simple, rarely branched, 6-10 dm tall, sparsely to densely hirsute below, more densely so above; leaves lanceolate, lance-linear, entire, hirsute or pilose; basal leaves 0.5-3.5 dm long, 0.5-4 cm wide; cauline leaves 0.5-2.5 dm long, 1-2.5 cm wide, petiolate below to sessile and much reduced above; heads conical to slightly hemispheric; phyllaries lanceolate, 7-15 mm long, 1.5-3.5 mm wide, hirsute, ciliate, 3-4 series, gradually passing into pales; ligules drooping, 4-9 cm long, 4-7 mm wide, purplish-pink, rose-colored, or white; pales 8-12 mm long, awn 2-3 mm long; achenes 4 mm long, glabrous, pappus a slightly toothed crown; pollen yellow, 22.5-24.5 μ in dia. (ave. 24.2); chromosome number n= 11.

DISTRIBUTION: rocky open wooded hillsides and prairies. North central Arkansas, eastern Missouri, western Illinois, and west-central Kentucky. Fig. 3.

TYPE: MISSOURI: Crawford Co.: 4 mi n Dillard, rocky open bank at edge of woods, 7 June 1960, *R. L. McGregor 15636* (KANU!).

REPRESENTATIVE SPECIMENS EXAMINED: ARKANSAS: opening in mixed woods, 10.2 mi e Mt. Home, 2 June 1960, *Harms 319* (KANU). Independence Co.: dry ridge thickets, Pleasant Plains, 27 June 1948, *Demaree 26938* (SMU). ILLINOIS: Piatt Co.: along road near Monticello, 12 June 1960, *Jones 30376* (ILL). Richland Co.: along roadside, 2 mi n Olney, 21 June 1947, *Scherer 246* (ILL). KENTUCKY: Edmonson Co.: vicinity of Mammoth Cave, May 1899, *Palmer* (US). Hart Co.: road cut, Mammoth Cave Ferry Road, 26 June 1947, *Lix 281* (US). MISSOURI: Butler Co.: rocky bank, 5 mi nw Poplar Bluff, 19 June 1962, *McGregor 17154* (KANU). Howell Co.: grassy ridge, 2.3 mi nw Willow Springs, 3 June 1960, *Harms 323* (KANU). Phelps Co.: rocky open wooded area, 5 mi n Rolla, 8 June 1960, *McGregor 15649* (KANU). St. Francois Co.: along Plattin Creek, Koester Springs, e Koester, 4 June 1941, *Steyermark 28797* (F).

Echinacea simulata is very similar to *E. pallida* and long has been included in the latter species. It was first detected when a study of pollen size of *E. pallida* revealed that plants now referred to as *simulata* had consistently smaller pollen and occupied a distinct geographic area. Further studies revealed that *pallida* was a polyploid with n=22 while *simulata* had n=11. The pollen of *pallida* is always white while that of *simulata* is yellow. Intensive field work in the areas where the two species merge revealed an overlap in range limited to five to ten miles. In this zone frequent sterile triploid hybrids are found. The role of *E. simulata* in developing the allopolyploid *E. pallida* is discussed under the latter species.

10. **Echinacea sanguinea** Nutt. Trans. Am. Phil. Soc. n. ser. 7:354. 1841.

Stems simple or with a few branches, 4-9 dm high, hirsute or nearly glabrous below, hirsute above to nearly glabrous; basal leaves petiolate, 10-24 cm long, 1-2.8 cm broad, blades elliptical, lower cauline leaves petiolate, upper sessile, elliptical or lanceolate, acute, leaves hirsute on both surfaces, entire; heads nearly hemispheric becoming slightly conic in fruit, 1.1-2 cm high, 1.7-2.4 cm broad; peduncle half or more the height of plant; phyllaries lanceolate to oblong-lanceolate, 7-10 cm long, hirsute, ciliate; rays rose-

colored to dark red, rarely white, 4-7 cm long, 3-4 mm broad; pales 8.5-10 mm long, awn 1.5-2 mm long; disk flower corolla 5.8-6.7 mm long, lobes 0.8-1.5 mm long; achenes 2-3.9 (3.0) mm long, pappus a low crown, teeth nearly equal in length; pollen grains yellow, 19-23 μ in dia. (ave. 21.5); chromosome number n=11.

DISTRIBUTION: Sandy, open, pine barrens and prairie. Southeastern Okla., southwestern Arkansas, western Louisiana and east Texas. Fig. 3.

TYPE: OKLAHOMA: "The plains of Red River, near the confluence of the Kiamesha." *Nuttall* (BM, Photo!).

REPRESENTATIVE SPECIMENS EXAMINED: ARKANSAS: Miller Co.: pine woods, n Texarkana, 8 June 1898, *Eggert* (MO). LOUISIANA: Beauregard Parish: edge of sandy pine woods, 3.7 mi s Longville, 20 May 1956, *Shinners 23532* (GH, SMU). Jeff Davis Parish: low prairies, Jennings, 15 May 1915, *Palmer 7632* (MO, NY, US). Vernon Parish: w edge of Leesville, 12 May 1960, *McGregor 15571* (KANU). OKLAHOMA: Choctaw Co.: sandy open forest, 4 mi s Fort Towson, near mouth of Kiamichi River, 20 May 1961, *McGregor 16850* (KANU). TEXAS: Angelina Co.: sandy open pine woods, 2.6 mi s Lufkin, 12 May 1960, *McGregor 15557*(KANU). Bowie Co.: open woods, 2 mi e Maud, 11 May 1949, *Cory 55965* (SMU, US). Hardin Co.: 4 mi sw Silsbee, 9 May 1947, *Whitehouse 31589* (SMU). Harris Co.: prairies, Houston, 23 May 1917, *Palmer 12027* (GH, US). Jasper Co.: clearing in pine-oak woods, 6.5 mi e Jasper, 12 May 1960, *McGregor 15569* (KANU). Polk Co.: sandy open pine woods, 2 mi w Camden, 31 May 1954, *Tharp, Turner, Johnston, 54729* (OKLA, SMU, TEX). Wood Co.: sandy pine land, n Crow near Lake Ellis, 14 June 1940, *E. L. & Amelia Lundell 9476* (GH, SMU).

Echinacea sanguinea was described by Nuttall (1841) with a clear and adequate description. He gave the habitat as "The plains of the Red River near the confluence of the Kiamesha River." The latter river is now known as the Kiamichi and joins the Red River in southcentral Choctaw County, Oklahoma. The type specimen, in the Nuttall collection in the British Museum of Natural History, consists of a fragmentary piece of stem and battered capitulum and is a most unsatisfactory type. No other Nuttall collections of this species have been located. I have collected the species from the type locality which is also the northern extent of its range.

The identity of *E. sanguinea* has been overlooked perhaps because few specimens were present in major herbaria. Fernald (1900) considered it as a synonym of *E. pallida*, and Sharp (1935) listed it as a synonym of *E. angustifolia*. Otherwise no other reference to the species has been found. Most collectors have determined specimens as *E. pallida*. It differs from the latter in having hemispheric heads, slender stems, narrower rays, elliptic radical leaves, yellow pollen, and is a diploid. Its habitat is open woodlands and open sandy fields.

11. **Echinacea tennesseensis** (Beadle) Small. Man. Southeast Fl. 1421. 1933.

Brauneria tennesseensis Beadle. Bot. Gaz. 25:359. 1898.
Echinacea angustifolia var. *tennesseensis* (Beadle) Blake. Journ. Wash. Acad. Sci. 19:273. 1929.

Stems simple or with one or two branches, 1-4 dm high, hirsute or somewhat tuberculate hirsute; basal and lower cauline leaves petiolate, 5-17 cm

long, 5-10 cm wide, hirsute to tuberculate-hirsute, narrowly long-elliptical to linear-lanceolate, 3-nerved, acute, attenuate at base, upper leaves sessile; heads 1-2 cm high, 1.5-2.5 cm broad; phyllaries in 3-4 series, 5-9 mm long, 2 mm broad, pales 10-12 mm long, awn 2-3 mm long; disk corolla 5.5-6.5 mm long, achenes 4-sided, 4.5-5 mm long, pappus a low crown with a prominent tooth at each corner.

DISTRIBUTION: Dry, gravelly hills and barrens near LaVergne, Tenn.

TYPE: TENNESSEE: Rutherford County; near LaVergne, gravelly hill, just in flower, 19 Aug. 1897. *H. G. Eggert* (holotype US!; isotypes GH!, MO!).

REPRESENTATIVE SPECIMENS EXAMINED: TENNESSEE: Rutherford Co.: dry open soil, no loc., 5 June 1936, *McVaugh 1452* (GA); Lavergne, 14 June 1897, *H. Eggert* (NY, TEX, US); stony hills, no loc., 14 July 1897, *H. Eggert* (GH); Lavergne, 14 July 1897, *H. Eggert* (MO); cedar glades, no loc., 14 July 1897, *H. Eggert* (NY); Lavergne, 18 Aug. 1897, *H. Eggert* (MO); gravelly dry hills, near Lavergne, 19 Aug. 1897, *H. G. Eggert* (GH, MO, US); cedar barrens, July, Lavergne, *Dr. A. Gattinger* (NY); cedar barrens, Lavergne, 15 Aug. 1878, *A. Gattinger* (GH); very sterile soil, cedar barrens, Aug. 1878, *A. Gattinger* (MO).

Beadle (1898) described *Brauneria tennesseensis* on the basis of plants collected by H. Eggert on August 19, 1897, from a dry, gravelly hill near LaVergne, Tenn. He described the species as "closely related to *B. pallida* from which it may be known by its smaller size, very hispid stem and leaves, longer and narrower achenes, by the later season of flowering, and the spreading scarcely drooping rays." At the time of Beadle's publication it was commonly held that *B. pallida* included *E. angustifolia*. It is strange that Beadle compared his new species only with *pallida* as his description is nearly identical with that of *E. angustifolia* except for the later flowering date. Fernald (1900) clearly recognized this and, while recognizing both *Echinacea pallida* and *angustifolia* as valid species, he merged *E. tennesseensis* with *angustifolia*. Blake (1929) made *tennesseensis* a variety of *angustifolia* and this was recognized by Sharp (1935).

The first collections were by Dr. A. Gattinger in July and August of 1878. H. Eggert apparently made collections in June, July and August of 1897 and Rogers McVaugh in June of 1936. I searched for the species during the months of June, July and August in the years 1959, 1960, and 1961, but without success. In her extensive work in the Cedar Barrens, Dr. Elsie Quarterman (personal correspondence) never found *E. tennesseensis*.

The dates and curious label data of the Eggert and Gattinger collections leave me uncertain as to possible errors in labeling and collection dates. Of the June 14, 1897, collections of H. Eggert, 3 sheets with one set of data are found in three herbaria (NY, TEX, US). Three of Eggert's collections of July 14, 1897, with different data are at GH, MO, and NY. Eggert's August 18, 1897, collection also consists of three sheets of which two are identical and are at MO and PH while the third is at MO. The August 19, 1897, collection consists of three identical sheets at MO, GH, and US. Thus three sheets were

prepared from the June 14, July 14, August 18, and August 19 collections. It is apparent that little weight can be given to dates of collections made by Eggert and Gattinger. However, the McVaugh collection and the June 14, 1897, collections of Eggert indicate the species blooms in June and this is in line with all other taxa of the genus which grow on open habitats.

Until living material can be found, it seems best to recognize *E. tennesseensis* as a very rare or possibly extinct species endemic to the Cedar Barren area of central Tennessee. It is morphologically similar to *E. angustifolia* var. *angustifolia* but is smaller in all respects. The pubescence is softer, pollen grains smaller (18.5 μ vs. 21 μ), and stem more leafy.

EXCLUDED TAXA

Echinacea atrorubens Chap=*Rudbeckia graminifolia* (T. & G.) Boynton and Beadle.
Echinacea atrorubens Nutt. var. *graminifolia* T. & G.=*Rudbeckia graminifolia* (T. & G.) Boynton & Beadle.
Echinacea chrysantha Sch. Bip.=*Rudbeckia chrysantha* Klatt.
Echinacea dicksonii Lindl=*Iostephane heterophylla* var. *dicksonii* (Lindl.) W. M. Sharp.
Echinacea dubia Knowles & Wescott.=*Iostephane heterophylla* (Cav.) Benth.
Echinacea heterophylla (Cav.) D. Don=*Iostephane heterophylla* (Cav.) Benth.
Echinacea hybrida Hort. ex. Bull. Jard. Bot. Brux. 9. Fasc. Suppl. 1, p. 5. 1931. Is probably a cultivar of *E. purpurea* but disposition is uncertain.
Echinacea napifolia Sweet=*Iostephane heterophylla* (Cav.) Benth.
Echinacea purpurea var. *serotina* Bailey=*Rudbeckia purpurea* var. *serotina* (Nutt.) Nutt.

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Distribution and Variation of *Etheostoma spectabile* (Agassiz) (Percidae, Teleostei)

DONALD A. DISTLER[1]
Department of Zoology
University of Kansas

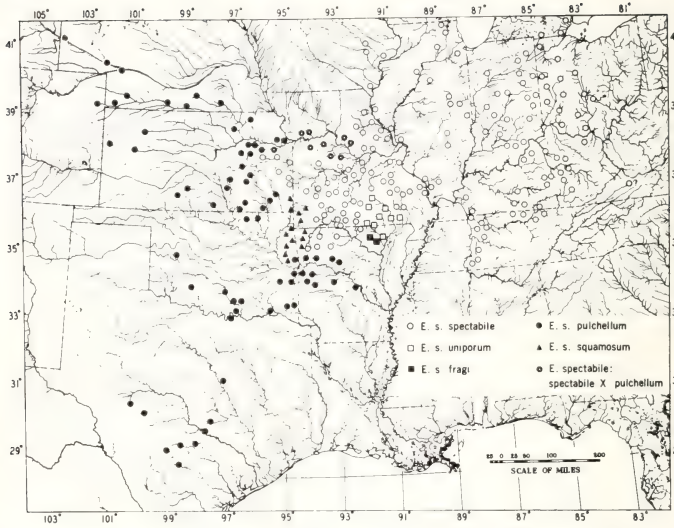
ABSTRACT

Etheostoma spectabile, the orangethroat darter, is a small, bottom-dwelling inhabitant of upland, hardwater streams in the Mississippi River System and western Coastal Province. This study has attempted to determine the present range and phenotypic variation of the species, to determine the fertility and character stability in progeny resulting from laboratory crosses between phenotypically distinct populations and within such populations, and to interpret the zoogeography of the species so far as it can be inferred from biological and geological evidence now available. Five subspecies are recognized: *E. s. spectabile, E. s. pulchellum, E. s. squamosum, E. s. fragi,* and *E. s. uniporum.* The distributions, areas of intergradation, and probable evolutionary histories of the taxa are discussed in relation to geologic changes that may have effected these phenomena.

INTRODUCTION

The orangethroat darter, *Etheostoma spectabile* (Agassiz), is a small percid fish inhabiting hardwater, gravelly streams of the Edwards, Ozark, and Interior Low plateaus and adjacent Central Lowlands of North America (Map 1). The tribe Etheostomatini, subfamily Percinae, to which the orangethroat belongs, is composed of about 100 species that are endemic to the Atlantic drainage of North America (one species in the Pacific drainage of Mexico; *cf.* Meek, 1904). The members of this tribe have the air bladder reduced or absent, and are thereby adapted to a bottom-dwelling mode of life. Most occur in parts of streams with weak to moderately strong currents. The orangethroat has posed systematic problems for ichthyologists since its description in 1854. Unfortunately, this species has been recognized in the

[1] Present address: Biology Department, Wichita State University, Wichita, Kansas.



MAP 1. Distribution of *Etheostoma spectabile*. Symbols indicate streams from which one or more collections of orangethroats have been examined or taken. Records in Indiana are partly from Gerking (1945:94) and in Ohio partly from Trautman (1957:597). Localities where intergrades and hybrids have been collected are omitted with the exception of the extensive zone of intergradation between *E. s. spectabile* and *E. s. pulchellum*.

literature and catalogued under various names. Early workers considered it to be conspecific with *Etheostoma caeruleum* Storer, the rainbow darter. This arrangement remained until Trautman (1930) established the specific distinctness of the two darters. Attention has been given the orangethroat in faunal studies and in keys for identification. Winn (1958) described its breeding behavior and ecology. Hubbs (1955) and Linder (1955) reported the occurrence of natural hybrids between the orangethroat and other darters. Clark Hubbs and his associates at the University of Texas have utilized this darter in studies of experimental hybrids. Collette (1965) commented on the phylogenetic significance of breeding tubercles on nuptial males of this and other species of percids.

Although much attention has been given the orangethroat in previous investigations, the relationships of populations throughout the range remain obscure. Hence a study of variation permitting refined diagnosis of the species is in order. At the time this study was begun, the orangethroat was considered in the literature to be composed of two subspecies: *E. s. spectabile*, the northern orangethroat, of the Ozark and Interior Low Plateaus and adjacent Central Lowlands, and *E. s. pulchellum*, the plains orangethroat, of the Great Plains and adjacent Central Lowlands. Hubbs and Lagler (1958),

in a comment on the range of *E. s. spectabile*, suggested the possibility of further subspeciation south of the Ohio River System. Two variants that I describe as the subspecies *E. s. squamosum* and *E. s. uniporum* from the Ozark region were recognized by earlier workers. Carl Hubbs was aware of both variants on the basis of specimens in the collections of the University of Michigan Museum of Zoology, and J. D. Black (unpublished doctoral dissertation, University of Michigan, 1940) mentions one of them.

The purposes of this report are to (1) determine the present range and investigate morphological variation of the orangethroat, (2) elucidate the evolutionary history of the species insofar as it can be inferred from geological and zoogeographic evidence now available, and (3) demonstrate the degree of interfertility, character-stability, and relationships of morphologically distinguishable forms as indicated by experimental crossings of individuals representing several populations.

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METHODS

Characters studied included 32 morphometric and 25 meristic features

determined for small series (20-30) from localities throughout the range of the species. To minimize the effects of allometric growth on the data, only specimens larger than 30 mm in standard length were used. Counts and measurements were made by methods given in Hubbs and Lagler (1958) unless otherwise indicated. Data for each sex were analyzed separately and later combined unless there was significant difference between sexes.

Most morphometric data have scant diagnostic value because sexual dimorphism, breeding condition, state of preservation, and measuring error (large in proportion to the total length of these small fish) tend to mask differences between geographic variants. Therefore measurements are omitted from the descriptive accounts that follow.

Coloration and the following characters seem most useful for defining geographic variation and revealing trends within and between river systems. *Gill membranes* are indicated to be separate to moderately conjoined, based on the distance from the tip of the snout to their union. If this distance, measured with dividers, was less than the distance from the tip of the snout to the posterior orbital rim, an index of 0 was recorded; if the distance exceeded this, but terminated within the postocular sinus (Branson and Moore, 1962), a 1 was recorded; if the distance extended beyond the postocular sinus, a 2 was recorded. *Lateral line scales* were counted on the left side only. At first, counts from males and females were averaged separately; then, these counts were combined because only small series had means that were not within one scale of each other. *Pored lateral line scales* were counted as above. *Diagonal scales* were counted on the left side, beginning at the origin of the soft-dorsal fin and proceeding downward in the diagonal series to the anal fin. *Scales above the lateral line* were counted as above, except that the count was terminated in the scale row above the lateral line.

Anterior squamation is represented by indices 0 through 3 for each part of the fish under consideration. An index of 0 was recorded for any part devoid of scales. For the cheek, one scale of two rows of scales below or behind the orbit was considered "lightly scaled" and given an index number of 1; three or four rows, "moderately scaled," as index of 2; more than four rows, "well scaled," an index of 3. For opercle and nape, less than 50 per cent scaled, an index of 1; more than 50 per cent scaled, but not completely scaled, an index of 2; fully scaled, an index of 3. For the breast, when scaled before either the pectoral or pelvic fin but not both, an index of 1; before both fins but not covering the posterior portion of the breast, an index of 2; covering posterior portion of the breast, an index of 3. In all regions embedded scales were included if they were evident without dissection. These indices were summed and divided by four to obtain an *anterior scale index*.

The *infraorbital canal* is interrupted (rarely complete) in the orangethroat. There are usually four (sometimes three or five) anterior pores associated with the lachrymal bone, an interruption, then one to five pores

associated with the orbital series of bones from the dermosphenotic anteriad. Because of the variable nature of the posterior set of pores, they are the only ones reported in this study. The *supratemporal canal* is often complete, having a single median and two dorsolateral pores, but may be widely to narrowly interrupted medially.

Lepidotrichs are of some diagnostic value and their number is discussed where clines appear in and between various river systems or geographic races. Counts reported are of dorsal spines, dorsal soft-rays, anal soft-rays, and pectoral rays. *Breeding tubercles* are variably present on males on the ventrolateral surfaces posterior to the breast, during the height of the breeding season; however, they show considerable variation as to location and degree of development. The *genital papilla of males* is usually conical, but the shape of the apex and degree of pigmentation vary throughout the range.

An attempt was made to give a complete literature record. In literature prior to 1930, I have included only those reports with an adequate description of the species or reports from localities where *spectabile* now occurs; nevertheless, some of the citations may refer to *E. caeruleum* or to mixed collections of *caeruleum* and *spectabile*.

Material examined is listed in my doctoral dissertation (1966), The University of Kansas, Lawrence, Kansas and in University Microfilms (Dissertation Abstracts 28: 1267, 1967), Ann Arbor, Michigan.

DESCRIPTIONS

Etheostoma spectabile (Agassiz)

Figure 1

Diagnosis. A species of *Etheostoma,* subgenus *Oligocephalus,* having an interrupted infraorbital canal, body depth greatest near origin of spinous dorsal fin, 11-12 pectoral rays, and, in nuptial males, bright orange branchiostegal membranes and usually absence of red on anal fin (when present, red in anal fin restricted to amorphic blotches, never the prevalent color).

Description. Body shape average to stout, oval in cross-section, back elevated, and caudal peduncle rather slender; head large, 3.0-3.8 in standard length; mouth average, subterminal to terminal, lower jaw included, upper jaw 3.1-4.0 in head-length; snout rather strongly decurved; eye average, 3.5-4.5 in head-length; gill membranes separate to moderately connected; dorsal spines 8-12, usually 9-10; dorsal rays 10-15, usually 12-13; branched caudal rays 10-15, usually 13-14; anal spines 2; anal soft-rays 4-8, usually 6-7; pelvic spine 1; pelvic soft-rays 5; pectoral rays 10-14, usually 11-12; infraorbital canal incomplete (usually 4 pores anteriorly and 1-5 posteriorly), rarely complete with 8-9 pores; lateral (temporal) canal with 5 pores; anterior nasal, posterior nasal, interorbital, coronal, and postorbital pores present; preoperculomandibular canal with 10 (rarely 9) pores; vertebrae 35-37, usually

36; top of head naked except for several small scales at junction of lateral and supratemporal canals; squamation of sides of head variable. Breast usually naked. If present, scales on head and breast often embedded and cycloid.

Base color brownish to olivaceous; dorsum and upper sides densely pigmented, variably lined or tesselated; males brightly colored with red or orange and blue or blue-green, base color of sides and ventrum often white; sides with 4-11 transverse bars from axil of pectoral fin to base of caudal fin, bars on postanal sides usually most prominent; in breeding males, bars dark blue or blue-green, spaces between bars bright orange or red; bars variably continuous or interrupted across ventrum; dorsum with 0-10 squarish, dark-brown saddles alternating and coalescent with or separate from lateral bars; spinous dorsal fin dark blue or green marginally, having a variably developed submarginal (and sometimes a basal) orange band; red or orange present in soft dorsal fin, often predominant color; caudal fin colorless to pale yellow, rays red in northern Ozarks; anal fin dark blue or green, anterior rays often colorless distally, ray-margins and breeding tubercles opaque white; pelvic fins blue- or green-black, margins and tubercles similar to those of anal fin; pectoral fins colorless to pale yellow.

Color in females more subdued than in males, pale reds and blues evident during breeding season; ventrum generally immaculate; anal and paired fins generally colorless.

Breeding tubercles variable in males; if present, appearing on one, several, or all of the following locations: anal spines and rays, pelvic spines and rays, lower rays of caudal fin, lower rays of pectoral fin, and ventral scales.

Genital papilla of males flattened, commonly subtriangular: distally may be acute, obtuse, rounded, emarginate, truncate, or acuminate; coloration variable. Papilla of adult females oblong and tubular, overlapping front of first anal ray, always immaculate.

HABITAT. Sluggish to moderately swift, shallow, hardwater streams with bottoms of sand, gravel, rubble, or bedrock. Inhabitant of riffles, raceways, shallow pools and backwater, occasionally in temperate springs.

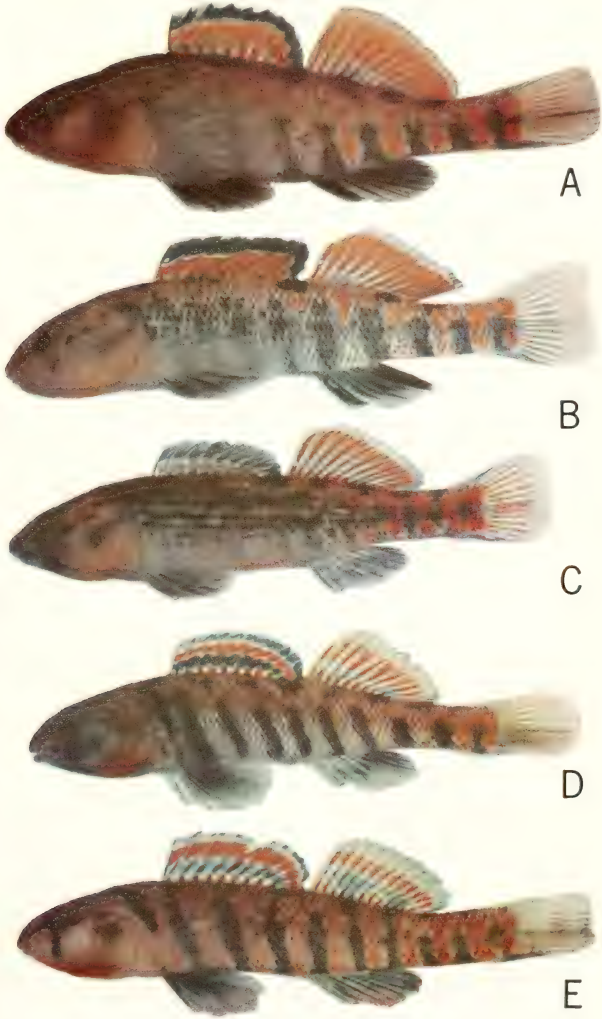
Etheostoma spectabile spectabile (Agassiz)

Northern Orangethroat Darter

Figure 1C

Poecilichthys spectabilis Agassiz, 1854, Amer. J. Sci. Arts, 17:304 (Osage River, Mo.).
Poecilichthys versicolor Agassiz, 1854, Amer. J. Sci. Arts, 17:304 (Quincy, Ill.). See Collette and Knapp (1967).

TYPES. Three sets of syntypes of *Poecilichthys spectabilis* Agassiz are extant; they are in the University of Michigan Museum of Zoology (UMMZ 86340, 8 specimens), the United States National Museum (USNM 120284,


A
B
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5 specimens), and the Museum of Comparative Zoology, Harvard University (MCZ 24503, 24520, 24722; 21 specimens.

A lectotype, male, 47.5 mm in standard length, is herein designated from the Michigan series and retains the original catalog number. A lectotype is designated because one specimen of *E. caeruleum* was present in the original series. The remaining paralectotypes in the Michigan set have been recataloged as UMMZ 179528 and the specimen of *E. caeruleum* as UMMZ 179529.

I have not seen the other type specimens, but those at the U.S. National Museum were checked by Leslie Knapp and Artie Metcalf and those at the Museum of Comparative Zoology by Bruce Collette. All were confirmed to be *E. spectabile*. Knapp (per. comm.) also confirms specimens of *P. versicolor* to be *E. spectabile*. See Collette and Knapp (1967).

Diagnosis. This subspecies can be distinguished from those of the western or *pulchellum* complex by a combination of the following characters: anterior region lightly to moderately scaled, index 1.5 (0.8-2.2); scales usually large, mean number of lateral line scales usually less than 48, of pored scales usually less than 30, diagonal scale rows usually 12 or less, scale rows above lateral line usually 5 or less (scale characteristics will separate most populations from *pulchellum* complex with exception of those in upper White River, Arkansas); branchiostegal membranes separate to slightly connected, index 1; in breeding males, fewer than 9 vertical blue bars or blotches, not continuous across ventrum except near base of caudal fin; blackish longitudinal lines strongly developed in northern Ozarks, less so in southern and eastern portion of range; belly of breeding males usually with discrete patches of red; spinous dorsal fin having three or more longitudinal bands of color, the distal two separated by a narrow colorless or white line, predominant color of fin bluish; soft dorsal having much blue (as well as red) pigment; caudal rays with or without red, membranes colorless.

Distinguished from *E. s. uniporum* by having sensory canals better developed (usually 2 or more pores in posterior segment of infraorbital canal, supratemporal canal complete, and pored scales more numerous); pectoral rays more than 11, and transverse bars nearly vertical, not well developed.

Distinguished from *E. s. fragi* by having anterior region less well scaled, body scales larger (lateral line and diagonal scale rows fewer), gular region uncolored, transverse bars less well developed in brightly colored males, belly not chevron-marked with orange, humeral spot less conspicuous, breeding tubercles usually present on nuptial males.

Coloration. *Breeding males:* The following composite account is based on specimens from the tributaries of the Osage River in Missouri, the type locality. Notable differences in coloration elsewhere in the range are discussed under river systems in which they occur.

Body scales, from dorsal midline to several scale rows below lateral line,

saturated basally with melanin, collectively producing pattern of continuous horizontal lines. Dorsum olive to reddish brown with 3-9 brownish black saddles from occiput to base of caudal fin, representing intensifications of melanin in horizontal lines. Upper sides reddish brown, lower sides pale blue to opaque white. Zero to 9 transverse bars representing intensifications of melanin in horizontal lines, usually suffused with blue on axilla and on post-anal sides; bars continuous across ventrum only near base of caudal fin. Interspaces between bars reddish orange, most intense posteriorly. Breast blue-gray changing to pink near insertion of pectoral fins, often saturated with fine melanophores. Belly having discrete, oblong salmon-red patches on each side of the ventral midline. Genital papilla blue-gray, saturated with fine melanophores. Cranial region blue-black; snout dark olive to reddish brown. Lips and anterior ½ of cheek blue-gray; suborbital bar blue-black; posterior half of cheek, sides of head, and operculum reddish orange, darkened by underlying melanin on opercle. Branchiostegal membranes brilliant red or orange. Chin and gular region blue-gray. Marginal ⅓-½ of spinous dorsal fin blue-black; beneath marginal band a narrow white or colorless band often suffused with deep red basally; beneath submarginal band a suprabasal gray or gray-blue band about ⅓ fin height; bands often separated by fine colorless or white lines. Soft dorsal fin also having 4 bands, but colors not so dense; marginal blue-gray, suprabasal blue-gray, and basal red bands usually narrow; submarginal red band usually wide; red best developed on membranes, blue on rays. Caudal rudimentary rays blue, principal rays usually red, occasionally alternating red and blue (barred appearance), rarely all blue; membranes usually colorless; base of fin with 2 orange or red spots in a vertical plane. Anal fin blue, occasionally with small red patches along base and more rarely along rays. Pelvic fins blue-black, having opaque whitish margins. Pectoral fins pink or pale yellow at base, rays occasionally paleblue, membranes colorless.

Non-breeding males: Chromatic colors subdued or lacking; melanins subdued. Pale blue persisting on suborbital bar, margin of spinous dorsal fin, base of anal fin, rudimentary caudal rays, and on caudal peduncle in association with transverse bars. Orange limited to branchiostegal membranes, interspaces on caudal peduncle, base of caudal fin, and thin submarginal band on dorsal fins. Transverse bars indistinct or absent. Horizontal lines often discontinuous.

Females: Mostly devoid of chromatic colors. In breeding specimens, branchiostegal membranes orange. Margin of spinous dorsal, base of posterior anal rays and vertical bars pale blue; bars more diffuse than in males. Branchiostegal membranes, gular region, and chin having fine, scattered melanophores. Soft dorsal and rays of caudal fin lightly barred with melanin. Ventrum immaculate, otherwise pattern of melanin like that of

males. Chromatic colors absent during non-breeding period except for faint red band in middle of spinous dorsal fin.

ADDITIONAL CHARACTERS (exclusive of populations in western Missouri River). The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral line scales* (Table 2): 44 (35-59); lowest mean number (39) in lower Cumberland River and (40) in Tennessee River, highest (52) in upper White River, Arkansas; differences in mean number of scales within river systems often far exceeds differences among them. However, the mean number of scales increases somewhat in major rivers northward from Tennessee River to Ohio River (40-45) and westward from Interior Low Plateaus to Ozark Plateaus (43-47). *Pored lateral line scales* (Table 5): 26 (12-42); lowest mean number (21) in Tennessee and lower Cumberland rivers, highest (33) in upper White River, Arkansas; similar to lateral line scales, differences within often exceed differences between river systems, also, there is an increase in the mean number of pored scales northward from Tennessee River to Ohio River (21-26) and westward from Interior Low Plateaus to Ozark Plateaus (24-27). *Diagonal scales:* 12 (9-17); modal number 12 through most of range, 11 in Tennessee River, 13 in upper White River; slight increase in mean from east to west and from south to north in eastern part of range. *Scales above lateral line:* 5 (4-8); modal number 5 through most of range, 6 in upper White River. *Anterior squamation* (Table 8): Cheek naked to well scaled, usually lightly scaled, mean index 1; lowest mean (0.9) in upper White River, highest (1.6) in Tennessee River. Opercle naked to well scaled, usually moderately scaled, mean index 2; lowest mean (1.1) in upper Green River, highest (3.0) in lower Cumberland River. Nape naked to well scaled, usually moderately scaled, mean index 2; lowest mean (1.2) in upper White River and (1.3) in upper Green River, highest (3.0) in Tennessee and lower Cumberland rivers, and (2.9) in lower Green River. Breast naked to moderately scaled, usually naked, mean index 0; highest mean (1.8) in lower Cumberland River. Mean anterior scale index 1.5; lowest mean (0.8) in upper White River and (0.9) in upper Green River, highest (2.2) in Tennessee and lower Cumberland rivers; mean index between major river systems decreases northward from Tennessee River to Ohio River (2.2-1.1), southward from Missouri River to White River (1.6-1.2), and westward from Interior Low Plateaus to Ozark Plateaus (1.5-1.4); differences within river systems far exceed differences between them. *Posterior infraorbital pores* (Table 12): 3 (1-5); modal number 3 through most of range. *Supratemporal canal* (Table 12): Usually complete throughout range; about 10 per cent of individuals east and 12 per cent west of Mississippi River with incomplete canals. *Gill membranes:* Separate to moderately connected; index 1 through most of range; index 0 in Ohio River system exclusive of Green, Cumberland, and Tennessee rivers. *Lepidotrichs:* Spinous dorsal 10 (8-12); soft dorsal 13 (11-15); anal soft-rays

7 (4-8); pectoral rays 12 (11-13). *Breeding tubercles:* Usually absent in Ohio River system and northward and in direct tributaries of Mississippi River; when present, restricted to anal rays. In remainder of range, tubercles present on anal and pelvic rays; also on ventral scales in Cumberland River, Missouri River, and upper White River in Arkansas; also along lower caudal rays in upper White River. *Genital papilla of males:* Acute, rounded, or acuminate; often truncate in central White River of Missouri and Arkansas. Usually stippled with fine melanophores.

Range. Tributaries of upper Mississippi River in southeastern Iowa (populations now extirpated) and northeastern Missouri; eastward through Illinois and Indiana to southeastern Michigan and western Ohio; southern tributaries of Ohio River from Kinniconick Creek (Kentucky) westward to Tennessee River; Osage River system of Kansas and Missouri, eastward and southward in Gasconade, Meramec, St. Francis, upper Black, and White rivers of Missouri; White River system in Arkansas from Ozark escarpment westward. Absent from Coastal Plain, Mississippi Embayment, and Appalachian Plateaus.

Intergrades. With *E. s. pulchellum* in eastern tributaries of Kansas River and Missouri River eastward to mouth of Osage River; possibly with *E. s. squamosum* in tributaries of upper White River in Arkansas.

Discussion. Unlike most other subspecies recognized herein, *E. s. spectabile* is a composite of weakly differentiated geographic races. Differences are significant among some populations, but variation is often clinal and zones of intergradation seem broad. In that part of the range east of the Mississippi River, my investigation was less intensive than in the Ozarks and western Central Lowlands; for some of the color descriptions in the eastern range, I have relied partly on notes and photographs by other investigators. A more thorough study of these eastern populations, especially in Kentucky and Tennessee, may reveal geographic races sufficiently distinct to be recognized as subspecies.

I use the terms race and subrace for populations less well defined than subspecies, but with diagnostic characters distinct enough to warrant mention.

Variation, particularly in color pattern, of characters which differ consistently from those of populations in the Osage River (the type locality) is discussed in the order of (1) streams draining the Ozark Plateaus east of the Missouri-Osage River confluence (generally north to south), and (2) streams east of the Mississippi River from north to south.

Variation west of the Mississippi River. Populations in the Casconade River are generally like those in the Osage River. Eastward, in the Meramec and in small, immediate tributaries of the Mississippi River, specimens have less intense horizontal lining and better developed vertical bars posteriorly than do those in the Osage River; bands of the spinous dorsal fin are sub-

equal in width and usually the caudal rays lack red pigment. In the Whitewater, St. Francis, and Black river populations, horizontal lines are broken and diffuse; the dorsum and upper sides are often dark and tesselated; blue is reduced throughout; red ventral pigmentation is developed extensively from the branchiostegal membranes to the caudal base. This bright red ventrum is least developed in specimens from the Whitewater River, reaching maximum development in populations of Black River and St. Francis River. As in the Meramec River specimens, bands of the spinous dorsal fin are subequal in width. In the Black River watershed from Cane Creek southward through Strawberry River, populations of orangethroats are recognized herein as two distinct subspecies; these are discussed later.

Westward in the White River drainage, populations of orangethroats are considered to be a southwestern race of *E. s. spectabile* because they resemble that subspecies more than they resemble the two subspecies in the tributaries of Black River alluded to above. The White River race is not a homogenous population, but on the basis of coloration and squamation it is divisible into two subraces or variants, one in the headwaters of White River above its confluence with Roaring River and one in the tributaries of White River from Roaring River eastward to the Ozark escarpment (sparsely distributed in tributaries east of the confluence of White River with its North Fork). The eastern subrace in White River differs as follows from Osage River populations: horizontal lines reduced to rows of dots and usually suffused with orange or deep red in interspaces between transverse bars, sometimes throughout; transverse bars of melanin variable, usually no more than blotches along lateral line; transverse bars of blue usually present along entire sides of breeding males; interspaces on lower sides gray or blue-white, occasionally with flecks of orange posteriorly; spinous dorsal fin with marginal and suprabasal blue bands partially to completely fused, basal red band narrow and often incomplete; soft dorsal fin predominantly blue (two thirds or more), red pigment limited usually to a narrow submarginal band; mean number of lateral line scales (43) lowest in any Ozarkian population; genital papilla of males truncate or mucronate, rarely rounded or obtuse.

In the western or headwater subrace in White River, horizontal lining is not so strong as in Osage River populations, but it is more evident than elsewhere in the range of the subspecies. These lines appear on at least four scale rows below the lateral line. Transverse bars of blue or blue-gray are darkened by melanin posteriorly. Anteriorly the lower sides are blue-white or gray, but the belly usually has an extensive orange patch. The suprabasal and marginal blue bands of the spinous dorsal fin are usually separated by a narrow red or red and white band; the blue-black marginal band is widest. The soft dorsal fin has 4 bands, but either blue or orange may be the dominant color. The largest area of tubercle-development is found in the western White River subrace. The lower caudal and outer surface of lower pectoral

rays are often tuberculate, as are anal rays, pelvic rays and ventral scales. The anterior scale index is low (0.8) compared with Osage and lower White River populations (both 1.5). The mean number of lateral line scales (52) is higher in the upper White River than anywhere in the range of the species except for populations of *E. s. pulchellum* in the Brazos River (53). The mean number of pored scales (33) is higher than elsewhere, except for populations of *E. s. pulchellum* in the Republican River (33) and Brazos River (34) and *E. s. fragi* in the Strawberry River (34).

The intermediate color patterns, tuberculate ventral scales, and tuberculate lower pectoral rays suggest that the upper White River subrace may consist of intergrades of *E. s. spectabile* and *E. s. squamosum* of the Illinois River (Arkansas River drainage). On the other hand, the anterior scale index is lower than, and the lateral line and pored scale counts of the western subrace of *E. s. spectabile* are higher than the corresponding values in the eastern White River subrace and *E. s. squamosum*, the supposed parental forms. I doubt that heterotic effects of interbreeding are responsible for these extreme values; laboratory crosses of stock from White River and Arkansas River exhibit no heterosis in the F_1 generation.

Barlow (1961) and others have suggested that slow embryonic development and/or low temperatures during formative periods increase meristic counts. Other environmental factors that influence meristic counts are summarized by Strawn (1961). Loren C. Hill (per. comm.) found an increase in the number of vertebrae in populations of *Etheostoma juliae* Meek from tributaries of upper White River. Gilbert Castro (per. comm.) found a similar increase in the number of lepidotrichs in populations of *Micropterus dolomieui* Lacépède from the same locality. Possibly low developmental temperatures are responsible for extreme meristic characters in upper White River.

Variation east of the Mississippi River. Orangethroats from streams in Illinois that flow directly into the Mississippi River closely resemble the Meramec-Big River populations in Missouri. Those from the upper Illinois and Kaskaskia rivers exhibit loss or reduction of horizontal lines (best developed in females). The transverse blue bars are variable. They may be restricted to the post-anal sides, or equally well developed on the trunk and caudal peduncle. Melanin associated with these bars, particularly on the post-anal sides, forms a subtriangular pattern, having the widest angle pointing anteriorly. Red is lacking on the caudal membranes, but they sometimes appear pale yellow or orange.

I have not examined live breeding males from Indiana, Michigan, and Ohio, but I surmise from preserved material that their coloration is similar to that of Illinois specimens. The marginal and suprabasal bands of the spinous dorsal fin are separated by a colorless or white band, a portion of which is usually suffused with red. There is a general decrease in the total

area of the body colored red and blue. Trautman (1957) mentions one difference in Ohio specimens in which the breast and ventral surface of the head are deep orange. Westward, the breast and underside of head (except for the branchiostegal membranes) are gray-white or blue-gray.

Reeve M. Bailey's field notes on specimens from Kentucky River agree generally with the description of Ohio specimens, but he notes that the distal portion of the caudal fin is tinged with orange, the pectoral fin with yellow-orange, and the anterior half of the breast is bright orange.

In specimens from Salt and Rolling Fork rivers in Kentucky, transverse bars are straplike and most evident on the post-anal sides. Orange is limited to the interspaces and best developed posteriorly. The breast and belly are usually immaculate, but orange is variably present on the belly (a few flecks to broad, oval patches). The submarginal red band of the spinous dorsal fin is reduced to a few red spots posteriorly, leaving the marginal and suprabasal bands separated by a white or colorless band; the basal red band is poorly developed. Horizontal lines are poorly developed on most specimens.

In my opinion, orangethroats from the Illinois and Kaskaskia rivers of Illinois, from the Lake Erie drainage, and from the entire drainage of the Ohio River with the exception of the Green, Cumberland, and Tennessee rivers of Kentucky and Tennessee represent a northeastern race of *E. s. spectabile*. I suspect that it originated from populations that found refuge in tributaries of the Ohio River during late Pleistocene glaciation. Members of this race seem more closely allied to each other than they do to populations in the Ozarks and populations in the Green, Cumberland, and Tennessee rivers.

Based on differences in coloration, anterior squamation, and body squamation, I recognize the orangethroats from Green (Barren), Cumberland, and Tennessee rivers of Kentucky and Tennessee as a southeastern race of *E. s. spectabile*. Populations in each of those three stream-systems seem distinctive also in some features of squamation and coloration, but I prefer not to recognize them taxonomically until a more thorough study can be made.

In the headwaters of Green River in Lincoln Co., Kentucky, orangethroats resemble those from Rolling Fork-Salt River except that the transverse bars are less well developed. The anterior scale index is low (0.9), the opercle and nape are usually sparsely scaled, and lateral line scales are usually 45 or more. Lower Green River (Barren River) populations have a high anterior scale index (1.9), the opercle and nape are well scaled, and the breast is lightly scaled; the lateral line scales average about 41. Adult males are often deep-bodied anteriorly. Transverse bars are represented by diffuse blotches of melanin along and slightly below the lateral line, from which pale, blue-gray bars extend dorsad and ventrad. Colored bars may appear from the axil of the pectoral fin to the base of the caudal fin but usually are best developed on the post-anal sides. The interspaces on the upper sides

are olivaceous with flecks of orange. Orange increases in extent posteriorly. Interspaces on the lower sides are gray-white and flecked with orange only on the caudal peduncle. Color radiates out of the orange spots at the base of the caudal fin along the principal rays. The rudimentary rays are pale green. The dorsum is often tesselated, contrasting sharply with the pallid base-color on the upper sides. The breast and belly are whitish except directly before the insertion of the pectoral fins, where the breast is cream-yellow. The principal evidence of horizontal lines is in the composition of the transverse blotches in females. The colored bands of the spinous dorsal fin, from the distal margin to the base, are as follows (numbers indicate approximate width of band as per cent of fin height): blue-black, 50; colorless or white, 20 (submarginal band of red lacking); blue-black, 10, and red 20.

I have not seen living specimens from the upper Cumberland River, but preserved individuals have a color pattern like Kentucky River specimens, though less dark. Transverse bars are more straplike than angular and there are faint horizontal lines in most specimens. Some individuals approach Barren River patterns of pigmentation. Interspaces are suffused with orange, but the anterior lower sides seem to have been bluish or gray-white. The upper sides are plain or tesselated. A thin, red, submarginal band is present in the spinous dorsal fin, but the caudal fin seems to lack red except at its base. There are usually more than 25 pored and 40 total lateral line scales. The anterior scale index is 1.3.

Preserved orangethroats from the lower Cumberland resemble Barren River populations. The horizontal lines are usually lacking or faint. The transverse bars, if not blotchlike, are best developed along the lateral line and a few scale rows below it. A few specimens are well banded along the entire sides. The dorsum except for the saddles is pale, the upper sides mottled or tesselated. The lower sides and belly are usually immaculate. No colors were preserved well enough to ascertain if a submarginal red band is present in the spinous dorsal fin. There are usually less than 22 pored and 40 lateral line scales. The anterior scale index is 2.2 because of an increase in breast squamation.

Orangethroats in the Tennessee River drainage seem to be restricted to tributaries of the lower Duck River (Piney River and westward), and to direct tributaries to the Tennessee River west of Waynesboro, Tenn. A single individual has been cataloged at the University of Michigan (UMMZ 96877) from the North Fork of Holston River in Virginia. Robert E. Jenkins (per. comm.) apprised me of a possible mixing of collections at UMMZ that may have been responsible for the inclusion of *E. spectabile* in the upper Tennessee River drainage. In 1928, Herbert R. Becker made a total of 34 collections in Virginia, Kentucky, Tennessee, Georgia, and Alabama. Evidently, most of the collections were sent to C. L. Hubbs at Michigan. In a letter to Becker dated 30 September 1928, Hubbs implied that a summer as-

sistant at UMMZ may have mixed up labels for specimens from some of Becker's collections and that he would welcome Becker's help in straightening out the trouble. However, Hubbs considered the record of *E. spectabile* from Virginia good because he had no evidence that labels from this accession had been mixed. Other than the alleged Holston River specimen (UMMZ 96877), specimens of *E. spectabile* were collected only from the Barren River drainage of Kentucky (UMMZ 96314, 4 specimens and UMMZ 96346, 20 specimens). No additional specimens have been collected from this locality. Ross and Carico (1963) in a survey of the North, Middle, and South forks of the Holston River, report no orangethroats from this drainage. Robert D. Ross (per. comm.) informed me that he has collected in headwaters of the Tennessee River as far west as Oak Ridge, Tenn., but has never found *E. spectabile*. Because of the absence of records from intervening streams and the existence of only one specimen, I believe the specimen labelled as having come from the Holston River is either an introduced individual or an erroneous locality record.

Preserved specimens from northern Duck River drainage exhibit moderately developed horizontal lines or rows of dots. The dorsum is pale except for saddles, and the upper sides are lined or tesselated. The transverse bars are blotch-like, having melanin best developed on the lower sides of the caudal peduncle. Some specimens are barred diffusely over the entire sides. The dark marginal and lighter suprabasal bands of blue on the spinous dorsal fin are often fused, at least posteriorly. The submarginal red band is lacking or poorly developed. There is evidence of an orange wash on the caudal fin. Except for the lined upper sides, these specimens resemble those from Barren River. The anterior scale index is 2.3. In specimens from Buffalo River (southern tributary of Duck River), horizontal lines are faint or absent. The transverse bars are diffusely blotched or subtriangular and often appear over the entire sides. The upper sides are pale in base color but mottled or tesselated and probably saturated with orange posteriorly. There is a progressive loss of scales on the cheek and breast from lower to upper Buffalo River (index 2.5 to 1.8). In Hardin Creek (an immediate tributary to Tennessee River with tributaries that interdigitate with those of the upper Buffalo River) specimens are similar to those of the upper Buffalo River in anterior squamation (1.8-2.0), but dusky, broken horizontal lines are evident on the upper sides.

Primary Literature Records and Misidentifications. This subspecies has been reported under the following names:

Poecilichthys spectabilis Agassiz (1854) original description, Osage River, Missouri—Nelson (1876) northern Illinois; Jordan (1876) in part, Indiana and Kentucky; Jordan (1877a) in part, Ohio River Valley; Jordan (1877b) in part, upper Mississippi River Valley and Lake Erie; Jordan (1877c) in part, White River, Indiana; Jordan (1878) Mississippi River Valley; Jordan and Brayton (1878) in part, Ohio and Illinois river basins; Jordan (1880) characters; Jordan and Gilbert (1882) characters, Mississippi River Valley; Jordan (1882) characters, ecology, Ohio; Trautman (1930) specific characters; Kuhne (1939) Tennessee; Collette and Knapp (1967)

catalog of type specimens. *Poecilichthys tersicolor* Agassiz (1854) original description, Quincy, Illinois—Collette and Knapp (1967) catalog of type specimens. *Astatichthys coeruleus* (Storer) —Vaillant (1873) in part, characters. *Astatichthys pulchellus* (Girard)—Vaillant (1873) in part, characters. *Etheostoma variatum spectabile*—Jordan and Meek (1885) characters, Lamine and Osage rivers, Missouri. *Etheostoma coeruleum spectabile*—Jordan (1885) Mississippi River Valley; Jordan and Gilbert(1886) White River, Arkansas; Meek (1891) in part, Missouri and White river basins in Missouri and Arkansas, characters; Meek (1892) Cedar River, Iowa; Meek (1894) White River, Arkansas; Hay (1894) in part, Indiana; Meek (1895) White River, Arkansas; Kirsch (1895a) Indiana; Kirsch (1895b) Ohio; Jordan and Evermann (1896) characters, Mississippi River Valley; Evermann and Cox (1896) in part, Missouri River Valley; Eigenmann and Beeson (1905) Indiana; Jordan (1916) in part, Indiana to Kansas. *Etheostoma caeruleum*—Kirsch (1892) in part, Tennessee River, Tennessee (2 specimens, UMMZ 61546, one is a male *E. s. spectabile*, the other, *E. caeruleum*); Hahn (1909) in part, Indiana (6 specimens, UMMZ 63003, 2 are *E. s. spectabile*, the remainder *E. caeruleum*); Forbes and Richardson (1920) in part, Illinois; Thompson and Hunt (1930) in part, Illinois. *Poecilichthys coeruleus spectabilis*—Hubbs (1926) Great Lakes Region; Hubbs and Ortenburger (1929) in part, Missouri and Kansas. *Oligocephalus coeruleus spectabilis*—Jordan (1929) characters, Missouri to Kansas. *Oligocephalus caeruleus*—Jordan, Evermann, and Clark (1930) in part, check list. *Poecilichthys spectabilis spectabilis*—Aitken (1940) Iowa; Hubbs and Lagler (1941) characters, distribution; Shoemaker (1942) characters, Wayne Co., Indiana; Gerking (1949) ecology, distribution, Indiana; Hubbs and Lagler (1949) characters, distribution; Shockley (1949) Boone Co., Indiana. *Etheostoma spectabile spectabile*—Harlan and Speaker (1951) characters, Iowa; Bailey (1951) characters, Iowa; Bailey and Gosline (1945) vertebral counts; Gerking (1955) characters, Indiana; Harlan and Speaker (1956) characters, Iowa; Bailey (1956) characters, Iowa; Trautman (1957) characters, ecology, distribution, Ohio; Hubbs and Lagler (1958) characters, distribution; Stegman and Minckley (1959) southern Illinois; Larimore and Smith (1963) distribution, Champaign Co., Illinois; Collette (1965) breeding tubercles; Collette and Knapp (1967) catalog. *Etheostoma spectabile*—Martin and Campbell (1953) Black River, Missouri; Eddy (1957) characters, distribution; Hubbs and Strawn (1957a) hybrid survival; Clark, Breukelman, and Andrews (1958) Lyon Co., Kansas; Hubbs (1958b) variation in egg complement; Winn (1958a) ecology, behavior; Winn (1958b) ecology, behavior; Hubbs (1959) hybrid combinations; Stegman (1959) southern Illinois; Bailey *et al.* (1960) common name; Larimore (1961) collecting success; Deacon (1961) eastern Kansas; Hubbs (1961b) gamete compatibility; Hubbs and Armstrong (1962) temperature tolerance; Fisher (1962) Missouri River near Rocheport, Missouri; Hubbs and Strawn (1963) temperature tolerance; Greeson (1963) Dix River, Kentucky; Pflieger (1966) habits of fry; Cross (1967) characters, habits, distribution in Kansas.

Etheostoma spectabile uniporum subsp. nov.

Current River Orangethroat

Figure 1D

Types. Holotype (KU 7478) an adult male 44.5 mm in standard length, collected by D. A. Distler and J. F. Downhower April 7, 1963, in Pigeon Creek, a headwater tributary of Current River, Sec. 8, T. 32 N, R. 7 W, Dent County, Missouri. Paratypes are 230 additional specimens (KU 7479, 7480) collected with the holotype.

Diagnosis. *E. s. uniporum* differs from other subspecies of *E. spectabile* in possessing a unique combination of the following characters: usually a single pore in posterior section of infraorbital canal, an interrupted supratemporal canal, less than ½ of lateral line scales pored, modal number of pectoral rays 11, and in coloration having transverse bars of equal intensity from axil of pectoral fin to base of caudal fin (anteriorly, bars slanting forward along plane of diagonal scale-rows, not subvertical as in other subspecies).

Coloration. *Breeding males:* The following data were taken from the

holotype and paratypes. Dorsum with 7-8 squarish saddles usually of equal intensity, but occasionally the saddle at posterior insertion of spinous dorsal and one at posterior insertion of soft dorsal darker than others. Upper sides brown to brick-red, usually with fine, discontinuous lines extending length of body. Lower sides blue-gray, rusty gray, or off-white where not crossed by bars; horizontal lines lacking except near lateral line. Transverse bars bright blue intensified by dense melanin, 2-3 scale rows wide and weakly continuous across ventrum, less often across dorsum; Current River specimens extreme in forward-slant of bars, Spring River specimens having more nearly vertical and occasionally wider bars. Entire sides lightly stippled with melanin. Humeral spot small but distinct, often iridescent blue or green, largest in specimens from Spring River. Breast gray-blue, gray, or white. Belly (between bars) rusty gray, gray-blue, or gray; incidence of a reddish ventrum somewhat higher in Spring River than elsewhere. Genital papilla and peritroct white, sometimes with a few melanophores. Dorsum of head dark brown. Cheeks bright blue, darkened with melanin. Pre- and postorbital bars narrow but distinct; suborbital bar diffuse in Current River, more distinct in Spring River. Lips, chin, and gular region gray or gray-blue; less blue in Spring River. Branchiostegal membranes bright orange, extending onto interopercle and subopercle, remainder of operculum brown or brownish orange. Spinous dorsal fin with 4 distinct bands generally separated from each other by narrow colorless or white lines: marginal blue, submarginal orange, suprabasal blue, and basal orange (suprabasal blue band generally widest); in Spring River, submarginal orange band much reduced, appearing only posteriorly or not at all, allowing variable fusion of marginal and suprabasal blue bands. Soft dorsal also four-banded, similar to *E. s. spectabile*. Rudimentary rays of caudal fin blue or blue-green, principal rays pale gray-yellow or gray-green; membranes mostly colorless; base of fin with 2 orange spots in a vertical plane, often coalescing. Anal fin blue-gray, fading distally; random flecks of orange occasionally appearing on fin. Pelvic fin blue-black, margin of rays white. Base of pectoral fins pale yellow or pink; rays near base pale blue to colorless, membranes colorless distally; fleshy axilla of fin orange.

Non-breeding males: Blues subdued or absent; lateral bars represented only by melanin, most dense on lower sides. Paired fins colorless. Caudal fin finely barred with melanin. Orange subdued. Melanin reduced.

Females: Blues absent or appearing only faintly. Orange limited to a fine submarginal band on spinous dorsal fin. Soft dorsal fin and caudal fin weakly barred with melanin. Sides with fine, discontinuous, horizontal lines. Transverse bars indistinct or wanting, except in Spring River, where often distinct.

ADDITIONAL CHARACTERS. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral*

line scales (Table 3): 45 (39-52). *Pored scales* (Table 6): 22 (10-32), less than in other subspecies except for populations of *E. s. spectabile* in the Tennessee and lower Cumberland rivers, which have an average of 21 pored scales. Specimens from Current and Eleven Point rivers have the lowest mean numbers within the range of *uniporum*. *Diagonal scales:* 12 (10-14), modal number 12 throughout range. *Scales above lateral line:* 5 (4-6), modal number 5 throughout range. *Anterior squamation* (Table 9): Cheek naked to well scaled, generally lightly scaled, mean index 1.2. Opercle naked to well scaled, mean index 1.7, a clinal increase from north to south (0.9 in Cane Creek to 2.3 in Spring River). Nape naked to well scaled, usually moderately scaled, mean index 1.6; in northern part of range (Cane Creek and Current River) nape usually lightly scaled, in remainder of range moderately scaled. Breast naked to moderately scaled, generally naked, mean index 0.2; little variation throughout range. Mean anterior scale index 1.2; 0.7 in northern part of range to 1.4 in southern part. *Posterior infraorbital pores* (Table 13): 1 (1-3), mean 1.4; modal number 1.0 in Cane Creek, Current and Eleven Point rivers; 2.0 in Fourche and Spring rivers. Lowest modal and mean number of subspecies complex. *Supratemporal canal* (Table 13): About ⅓ of all specimens examined with a complete canal; highest number of specimens having complete canals in Fourche and Spring rivers (*ca.* 60 per cent). *Gill membranes:* Separate to slightly connected, index of 1. *Lepidotrichs:* Spinous dorsal 10 (9-11); soft dorsal 12 (11-14); anal soft-rays 7 (6-8); pectoral rays 11 (10-12), lowest modal and mean number of subspecies complex. *Breeding tubercles:* Present on anal and pelvic rays of breeding males. *Genital papilla of males:* Generally with acute apex, little variation in shape.

Range. Black River drainage from Cane Creek, Butler County, Missouri, southward to Flat Creek, Lawrence County, Arkansas, in upland streams. Major tributaries include Current, Eleven Point, and Spring rivers.

Intergrades. In some characters with *E. s. spectabile* to the west and with *E. s. fragi* to the south. See below.

Discussion. In several respects, *uniporum* is the most neotenic member of the subspecies complex. The reduced infraorbital, supratemporal, and lateral line canals and a reduced number of pectoral rays probably are due to fixation of juvenile attributes. Collette (1962), in discussing populations of neotenic *Etheostoma fusiforme* (Girard), suggests that reduction of the number of pored scales, reduction of the number of infraorbital pores, and failure of the supratemporal canal to close probably is the result of the low productivity of lakes where these populations of neotenic darters occur. Productivity of a stream is largely dependent on the fertility of the soil over which it drains and composition of the channel in which it flows. The physicochemical properties of the Current and Eleven Point rivers seem no poorer than those of other streams draining the Ozarks. The Current and

Eleven Point rivers support a rich and varied fauna of both vertebrates and invertebrates and seem comparable to other Ozark streams where neoteny in the orangethroat is not evident. Within the range of *uniporum,* increase in the development of the acoustico-lateralis system southward may be due to the genetic influence of *E. s. fragi,* which has a better developed lateralis system than *uniporum,* or as Collette suggests, to an increase in productivity of the southern habitat.

Loss of scales from the opercle and nape may be a response to environmental conditions, but little experimental evidence for this is available. Of all members of the subspecies complex, only *E. s. pulchellum* has the anterior region more sparsely scaled.

Coloration of the spinous dorsal fin is somewhat like that of adjacent subspecies—*E. s. spectabile* in the upper Black River and *E. s. fragi* in the Strawberry River—except that the supra basal blue band is generally widest in *uniporum* and partially to completely fused to the marginal blue band in populations from Spring River. This fusion also is evidenced in populations of *E. s. spectabile* across the divide from Spring River in North Fork of White River. In males from Spring River the transverse bars are more nearly vertical and rarely slant as far forward as those in populations of *uniporum* from Eleven Point and Current rivers.

E. s. uniporum may have evolved from an Ozarkian stock of *E. spectabile* isolated in tributaries of Black River where *uniporum* now occurs. This probably occurred in post-Nebraskan time, after the Mississippi River shifted its course eastward from the Ozark highlands. Specimens reported as *Etheostoma coeruleum spectabile* by Meek (1891) from Spring River and its tributaries near Mammoth Spring, Fulton County, Arkansas, are referable to this subspecies.

ETYMOLOGY. The latin name *uniporum* is a substantive derived from *unus* (one) and *porus* (pore), and has reference to the single pore occurring modally in the posterior segment of the infraorbital canal.

Etheostoma spectabile fragi subsp. nov.

Strawberry River Orangethroat

Figure 1E

TYPES. Holotype (KU 7481) an adult male 44.0 mm in standard length, collected by D. A. Distler and J. F. Downhower, April 10, 1963, in Spring Creek, a tributary of Big Creek, Sec. 36, T. 16 N, R. 5 W, Sharp County, Arkansas. Paratypes are 145 additional specimens (KU 7482, 7483) collected with the holotype.

DIAGNOSIS. *E. s. fragi* differs from other subspecies of *E. spectabile* by possessing the following characters in a distinctive combination: gular region red in males, occasionally in females; blue on head restricted to sharply out-

lined suborbital bar; humeral spot distinct, iridescent blue-green; transverse bars on sides of body having little melanin, orange interspaces often continuous across belly in a chevron-shaped pattern; cheek well scaled, opercle and nape generally well scaled, breast usually lightly scaled, mean anterior scale index 2.5; breeding tubercles absent.

Coloration. *Breeding males:* Dorsum olivaceous to reddish brown, saddles narrow, usually indistinct. Sides with 10-12 transverse blue bars of equal density, little intensified by melanin; bars faintly continuous across belly, strongly so across post-anal ventrum; bars less often continuous across dorsum. Interspaces reddish brown or reddish gray on upper sides, paling ventrally and becoming orange on belly and ventrum of caudal peduncle. Horizontal lines fine, discontinuous, often indistinct, and generally limited to upper sides and a few scale rows below lateral line. Breast white, gray, or gray-orange. Dorsum of head brown; cheeks, sides of snout, and lips gray-yellow or white; suborbital bar bright blue, margins sharp; opercle brown fading to yellow ventrally; gular region, interopercle, ventral margin of opercle, and anterior $\frac{2}{3}$ of branchiostegal membranes bright orange (posterior $\frac{1}{3}$ colorless). Humeral spot distinct, often iridescent blue-green. Spinous dorsal fin 4-banded, with submarginal orange and suprabasal blue bands larger than marginal and basal bands; submarginal orange band usually widest, giving fin slight predominance of orange. Soft dorsal fin 4-banded, suprabasal blue band often well developed. Caudal rudimentary rays blue, usually most intense ventrally; principal rays gray-yellow or gray-blue; base of fin with 2 orange spots in a vertical plane; spots occasionally surrounded by a faint yellow ring, hence conspicuous. Anal fin gray-blue, blue fading distally; occasionally with flecks of orange on membranes or base of fin. Pelvic fins blue-black, with whitish margins. Base of pectoral fin gray to pale orange or blue, fleshy axilla of fin red, membranes generally colorless.

Non-breeding males: Blues subdued or lacking. Orange faded, but pattern distinct. Vertical bars most evident above and below lateral line. Ventrum often having orange bars or "chevrons." Horizontal lines somewhat more distinct than in breeding males.

Females: Dorsum and upper sides brownish yellow, having faint, discontinuous horizontal lines; lower sides, lips, cheek, throat, breast, and belly usually colorless except for suborbital bar on cheek (blue-gray). Sides occasionally with 10-11 pale blue-green, transverse bars, not intensified by melanin. Orange, if present, limited to narrow submarginal and basal bands on spinous dorsal fin, and on gular region. Rudimentary rays of caudal fin occasionally pale green. Soft dorsal and caudal fin weakly barred with melanin.

Additional Characters. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral*

line scales (Table 3): 50 (43-55), highest mean number in the species. *Pored scales* (Table 6): 35 (26-42), highest mean number in the species. *Diagonal scales:* 13 (12-15), modal number 13 throughout range. *Scales above lateral line:* 6 (5-6), modal number 6 throughout range. *Anterior squamation* (Table 9): Cheek lightly to well scaled, usually well scaled, mean index 2.9. Opercle lightly to well scaled, usually well scaled, mean index. 2.9. Nape lightly to well scaled, usually well scaled, mean index 2.7. Breast naked to well scaled, usually lightly scaled, mean index 1.4. Mean anterior scale index 2.5, highest in the species. *Posterior infraorbital pores* (Table 13): 3 (2-5), about 6 per cent having complete canals. *Supratemporal canal* (Table 13): Usually complete, about 6 per cent with incomplete canals. *Gill membranes:* Slightly to moderately connected; mean index 2. *Lepidotrichs:* Spinous dorsal 10 (8-12); soft dorsal 12 (11-14); anal soft-rays 7 (6-8); pectoral 12 (11-12), about 40 per cent of specimens with 11 rays. *Breeding tubercles:* Not evident in males in breeding condition; only member of species in which tubercles were not found. *Genital papilla of males:* Deltoid, with an acute apex.

RANGE. Strawberry River and its upland tributaries in northeastern Arkansas.

INTERGRADES. Possibly with *E. s. uniporum* in streams that interdigitate with tributaries of Spring River; in these streams, *E. s. fragi* has the anterior region least well scaled (index 2.1). Also *E. s. fragi* may intergrade with populations of *E. s. spectabile* in some lower tributaries of White River. Seven immature specimens (UMMZ 123615, *Poecilichthys s. spectabilis*) from Millers Creek, a tributary of White River near Batesville, Independence County, Arkansas possess patterns of pigmentation and head squamation suggesting intergradation between *E. s. spectabile* and *E. s. fragi*.

DISCUSSION. *E. s. fragi* is distinctive in coloration, but resembles *uniporum* more closely than any other subspecies. In squamation and the lack of breeding tubercles on males, *fragi* resembles an oligocephalid relative of the Coastal Plain and Mississippi Embayment, *Etheostoma asprigene* (Forbes). The latter darter, however, has a complete infraorbital canal and a mean number of one more pectoral ray than *fragi*. To my knowledge, *asprigene* has not been collected on or above the Ozark Escarpment. In Arkansas it has been recorded from the St. Francis Basin in gravelly streams draining minor uplands such as Crowley's Ridge, from the Cache River Trough near its confluence with White River, and from tributaries of Red River below the Ouachita Escarpment. I have never collected *asprigene* while seining for *spectabile*.

E. s. fragi may have evolved from a population of White River *spectabile* isolated in Strawberry River throughout most of the Pleistocene; however, I think that *fragi* is too distinct to have developed in this manner. It is alternatively possible that hybridization could have occurred between popula-

tions of *E. spectabile* in the Strawberry River and populations of a lowland scaly-cheeked darter (*E. asprigene*) before or shortly after the Mississippi River shifted eastward from the Ozark escarpment leaving an alluvial barrier to dispersal. The possibility exists also that *fragi* is really a neotenic *E. asprigene* that is undergoing reduction of the infraorbital canal. If so, I would expect a concomitant reduction of the supratemporal and lateral line canals, but this has not occurred.

Although *fragi* possesses characters common to several species, I judge that it is most closely related to *E. spectabile* populations (*uniporum*) of the lower Black River and that it has occupied the tributaries of the Strawberry River through much of the post-Kansan Pleistocene.

Etymology. The name *fragi* has reference to the Strawberry River where this subspecies occurs. The noun *fragum* (for Strawberry) is placed in the genitive singular modifying *Etheostoma*.

Etheostoma spectabile pulchellum (Girard)

Plains Orangethroat

Figure 1B

Oligocephalus pulchellus Girard, 1859b, Proc. Acad. Nat. Sci. Phila., 11:102 (Gypsum Creek, a tributary of the Washita River, Indian Territory, now Custer Co., Okla.).

Etheostoma arcus-celestis Crevecoeur, 1903, Trans. Kansas Acad. Sci., 18:177 (Vermillion River near Onaga, Pottawatomie Co., Kan.).

Type. A single, juvenile specimen, 25.0 mm in standard length, on which Girard based his description of *Oligocephalus pulchellus*, is in collections of the Museum of Comparative Zoology, Harvard University (MCZ 32950). This specimen was examined by Carl Hubbs (Hubbs and Ortenburger, 1929) and by Leslie Knapp who kindly took counts and measurements for me in June, 1962. Both Hubbs and Knapp confirm its identity with the western, plains representative of *E. spectabile*, but Knapp informs me that the specimen is in poor condition (body distorted, bleached, and left pectoral fin missing).

Girard (1859b) wrote that this specimen was captured in ". . . a tributary of Gypsum Creek, which empties itself into the Canadian River, by the party under Lieut. A. W. Whipple, while exploring the railroad along the 35th parallel." No tributary of the Canadian River, however, flows southward in the area concerned. Whipple (1856, pt. 2) in his log of the expedition writes, "Near Camp 30, we crossed Gypsum Creek, an affluent to the Washita, flowing south through bluff banks cut from an alluvial valley." Marcou (1856, pt. 4), geologist and mining engineer of the expedition, also places camps 30 and 31 in the Washita valley.

Grant Forman (1941), who edited and annotated Whipple's log of the survey, gives the Gypsum Creek locality (camp 30) as southeast of Arapaho, Custer County, Oklahoma. Streams draining this area are in the Washita

watershed; Beaver Creek, about 0.5 mile southeast of Arapaho, and Gyp Creek, about six miles southeast of Arapaho, are south-flowing tributaries of the Washita River that are now shallow. H. B. Möllhausen, topographer, artist, and naturalist of the expedition obscured the relationship of Gypsum Creek to the Washita River (established by Whipple and Marcou, and later confirmed by Forman) by stating in his diary of the journey (1858): "Scantily watered as the district was, we could manage every evening to reach a brook, which offered sufficient for our necessities, while our cattle found food on its banks. All these streams, including the most considerable of them, the Gypsum Creek, hastened in various windings to the Washita and Canadian. They were swarming with fish of many species, amongst which we particularly distinguished the *Chaetodon rostratus,* armed with its tremendous row of teeth: this creature appeared to share the dominion of the waters with the soft-shelled coriaceous turtle." In an account of *Moniana lutrensis,* Girard (1856) gave an accurate account of the locality ". . . Gypsum Creek, a tributary of the false Washita River . . ." (on maps available in 1856, the "false Washita" was the name used for the present Washita River in Oklahoma) but later (1859a, pt. 6) he reported an erroneous watershed-locality for *M. lutrensis* ("Tributary of Gypsum Creek, Canadian River") as he had for *O. pulchellus.*

On collecting trips in May, 1962, and May, 1964, to the headwaters of the Washita and southern tributaries of the Canadian along Whipple's route, I was unable to collect specimens of *E. s. pulchellum* in either drainage. The valley of Beaver Creek more closely resembles Whipple's description of the Gypsum Creek region than any tributary of the Canadian across the divide. The habitat in Beaver Creek seemed favorable for *E. s. pulchellum.* Because the Plains Orangethroat exists in similar habitat in tributaries of the lower Washita, it probably occupied Beaver Creek in times past. Prolonged drouths and recent excessive demands on groundwater have now reduced this and other tributaries of the Washita to streams of generally low flow or intermittency.

DIAGNOSIS. This subspecies can be distinguished from those of the eastern *(E. s. spectabile)* complex by its unique combination of the following characters: anterior region mostly naked, mean anterior index 0.6; scales small, mean number of lateral line scales usually more than 48, mean number of pored scales usually more than 30, diagonal scales usually 13, scales above lateral line usually 6, branchiostegal membranes moderately connected, index 2; in breeding males, 9 or more blue-green, transverse bars on sides of body from axil of pectoral fin to base of caudal fin, bars usually continuous across ventrum, especially posteriorly; horizontal lines poorly developed or absent; belly usually gray-blue or white, never with discrete red patches but sometimes with red pigment encroaching ventrally; spinous dorsal fin with 2 major longitudinal bands—a marginal, blue-black band

about $\frac{1}{3}$ of fin-height and a broad basal brick-red band; soft dorsal fin predominantly orange; caudal fin rays never red, membranes pale yellow to transparent. Differs from *E. s. squamosum* by usually naked cheek, opercle, breast, and much of nape and in less conspicuous horizontal lines and more distinct vertical bars on upper sides.

Coloration. *Breeding males:* Dorsum pale tan to brownish orange with 3-9 squarish dark saddles from occiput to base of caudal fin. Sides with 9 (6-11) vertical bars of melanin suffused with blue or blue-green, from axil of pectoral fin to base of caudal fin, most dark on lower and postanal sides; bars joining a single saddle dorsally or splitting to join two saddles dorsally, and ventrally either continuous or anastomosing with opposite bars. Interspaces on upper sides yellow, orange, or brownish orange; abdomen white, gray, or gray-blue (often orange or brick-red in Arkansas River drainage, from Poteau River eastward); interspaces of posterior lower sides mostly orange. Sides sometimes with poorly developed, broken, horizontal lines of melanin, best developed within vertical bars. Breast white, gray, or pale yellow. Genital papilla and peritroct grayish blue or green. Head brownish to dark olive dorsally. Snout, lips, and cheek anterior to suborbital bar pale yellow, orange or dark gray; suborbital bar short, rarely extending below preopercle, and often suffused with blue in Arkansas River drainage and southward; cheek posterior to suborbital bar colorless to yellow-gray. Operculum brownish orange. Branchiostegal membranes orange, paler than in eastern subspecies. Chin and gular region colorless to gray. Spinous dorsal fin with bluish or greenish black margin, about $\frac{1}{3}$ of fin-height; lower $\frac{2}{3}$ of fin bright orange to brick-red, separated from marginal band by a narrow colorless to white line; occasionally a narrow, usually incomplete, basal or suprabasal blue-green band best developed anteriorly; lower dark band seldom as dense as marginal band and seldom separated from orange by transparent or opaque areas. Soft dorsal fin mostly orange except for narrow, dusky-blue margin (best developed posteriorly) and a better developed, but often incomplete, basal or suprabasal blue or blue-green band; marginal band separated from orange by fine transparent line; lower blue band usually separated from orange dorsally by transparent areas located on lower $\frac{1}{3}$ to $\frac{1}{2}$ of fin rays and a small portion of adjacent membranes. Rays of both dorsal fins often less saturated with orange than membranes, and these areas first to fade in post-breeding condition. Rudimentary rays of caudal fin blue or blue-green; principal rays dark gray, blue, blue-green, or pale yellow; base of fin with 2 orange spots in a vertical plane, membranes colorless to pale yellow. Anal fin blue or blue-green, anterior rays and membranes often gray to colorless distally; occasionally small, amorphic, orange blotches on anal fin; breeding tubercles and ridges on anal fin-rays opaque white. Pelvic fins black, suffused with blue or blue-green, margin of rays usually opaque white, margin of fin grayish. Pectoral fins colorless

to pale yellow. Chromatic colors, when present on pectoral, pelvic, anal and caudal fins, usually best developed on base of fin and fading distally.

Non-breeding males: Orange subdued, blues much subdued or lacking. Vertical bars variably contracted or diffuse but never lacking. Anterior region pale except for dark cranial portion. Branchiostegal membranes pale orange. Dorsum light olive or tan with subdued darker saddles. Anal and pelvic fins transparent. Faint melanin on caudal and soft dorsal rays sometimes producing a weak barred effect.

Females: Orange usually limited to basal band on spinous dorsal fin but occasionally appearing faintly on soft dorsal fin. Branchiostegal membranes sometimes orange, usually colorless. Blue-green limited to lower sides of caudal peduncle, in association with vertical bars. Barred effect on caudal and soft dorsal fin more distinct than in males. Non-gravid females lack all chromatic colors.

ADDITIONAL CHARACTERS. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral line scales* (Table 4): 50 (41-61), a slight increase in mean number from north to south for each major river system except Red River; no consistent east-west gradient, although individual streams in major river systems may exhibit variation from headwaters to mouth. *Pored lateral line scales* (Table 7): 31 (21-42), mean number highest in Republican River (33); increase in mean number (31-32) from east to west in Arkansas River. *Diagonal scales:* 13 (11-16), modal number 13 throughout range, although 14 not uncommon. *Scales above lateral line:* 6 (5-7), little variation in mean number. *Anterior squamation* (Table 10): Cheek naked to lightly scaled, mean index 0.7; lowest mean (0.2) in upper Kansas River, highest (1.0) in Brazos and Colorado rivers; slight increase in mean from upper to lower Kansas River (0.2-0.8). Opercle naked to lightly scaled, usually naked, some specimens in lower Kansas and lower Red rivers moderately to well scaled (see DISCUSSION), mean index 0.3; lowest mean (0.0) in Brazos, Colorado, and Guadalupe rivers, highest (1.5) in lower Kansas River. Nape naked to well scaled, usually lightly scaled, mean index 1.3; lowest mean (0.9) in Brazos and upper Arkansas rivers, highest (2.0) in lower Kansas River. Breast naked (occasional specimens in lower Kansas River having one to several scales), mean index 0.0. Mean anterior index 0.6; little difference in mean between major river systems; within river systems lowest mean (0.4) in upper Kansas and upper Arkansas rivers, highest (1.1) in lower Kansas River. *Posterior infraorbital pores* (Table 14): 3 (1-4) modal number 2 in eastern Arkansas River. *Supratemporal canal* (Table 14): Usually complete, but increase in per cent incomplete from south to north throughout range, and from east to west in Arkansas River. *Gill membranes:* Moderately connected, index 2, except in eastern Kansas River where index is 1. *Lepidotrichs:* Spinous dorsal 10 (8-12) except in Republican River (9): soft

dorsal 13 (11-15); anal soft rays 7 (5-8) except in eastern Arkansas River (6); pectoral rays 12 (11-13). *Breeding tubercles:* Anal and pelvic lepidotrichs having ridges or tubercles (in specimens examined from Texas, not at peak of breeding condition, only anal rays tuberculate); tubercles on lower rays of pectoral fin and on ventral scales of specimens from eastern Kansas River and upper Mulberry River (eastern Arkansas River drainage). *Genital papilla of males:* Finely punctulated with melanin and suffused with blue or blue-green; usually deltoid in shape; apex obtuse, truncate, rounded, or acuminate.

Range. North Platte River of western Nebraska; Republican River of Colorado, Nebraska, and Kansas; Arkansas River from about Garden City, Kansas, to Ozark escarpment west of Little Rock, Arkansas, except in streams draining Springfield Plateau, where replaced by *E. s. squamosum;* Red River (mostly its northern tributaries) from Wichita Mountains eastward to Little River (southeast Oklahoma); Brazos, Colorado, Guadalupe-Medina rivers of Texas on Comanche and Edwards plateaus and southeastward to Balcones Escarpment.

Intergrades. With *E. s. spectabile* in southern tributaries of Kansas River eastward to confluence of Missouri and Osage rivers; with *E. s. squamosum* in lower tributaries of Neosho and Spring rivers in southeastern Kansas, in Illinois and Grand (Neosho) rivers near their confluence with Arkansas River, and in Sallisaw Creek (Arkansas tributary east of Illinois River confluence) in northeastern Oklahoma.

Discussion. The Plains Orangethroat shows comparatively little phenotypic variation throughout its range, with the exception of populations in the eastern Kansas, eastern Arkansas, and eastern Red rivers.

Most specimens in tributaries of the eastern Kansas River resemble those to the west and south but possess some characteristics of the eastern subspecies, *E. s. spectabile* (more squamous anterior region). The westernmost evidence of intergradation in color pattern is in semi-isolated tributaries of the Wakarusa River (Lone Star Lake), Douglas County, Kansas. Here coloration strongly resembles that of *E. s. spectabile* and squamation that of *pulchellum*; or, in other specimens, both characteristics are intermediate between the subspecies. Less than ten per cent of specimens collected just below Lone Star Lake have anterior scale characters of *E. s. spectabile;* usually all possess the coloration of *pulchellum*. The color pattern of *pulchellum* generally is dominant eastward to the Lamine River of Missouri where the color pattern is again intermediate and squamation approaches that of the nominate subspecies. In the Petite Saline River, Missouri (next drainage east of Lamine River), the color pattern of *E. s. spectabile* is more evident, although the dense melanin of the western subspecies remains; most males have pink belly patches and horizontal lining is moderate to strong; vertical bars are less dense and often are interrupted ventrally;

squamation of the body commonly is like that of the eastern subspecies anteriorly and like that of the western subspecies posteriorly. In the Moniteau and Moreau drainages, Missouri, coloration usually is that of the eastern subspecies, but vertical bars and horizontal lines are about equal in density. Posterior squamation (scales above lateral line; diagonal scales) in the Moniteau usually is that of *pulchellum* and in the Moreau usually is that of *E. s. spectabile*.

In northern tributaries of the Missouri River, I found no orangethroats farther west than Ray and Caldwell counties, Missouri; these are intergrades resembling mostly *pulchellum* in coloration, but intermediate in squamation between *E. s. spectabile* and *pulchellum*. In Howard County and eastward, orangethroats resemble representatives from Lamine River more closely than specimens from streams more nearly opposite them to the south, especially with regard to color pattern; the spinous dorsal fin may be like that of either subspecies or intermediate, the soft dorsal fin generally is pigmented like that of *pulchellum*. Horizontal lining is diffuse or absent in 70 per cent, faint in 20 per cent, and intense in 10 per cent of the 54 specimens examined. Most males have tuberculate anal and pelvic fins. Vertical bars are strongly developed. Squamation is intermediate but nearer that of the nominate subspecies.

In a cursory examination of specimens from the zone of intergradation, I could assign less than 10 per cent to one subspecies or the other. A more thorough investigation revealed evidence of intergradation in these few individuals.

Slight influence of the eastern subspecies can be seen westward in the Blue, Republican, and Platte rivers; anterior scale indices are higher than elsewhere in the range of *E. s. pulchellum,* the highest values being in the eastern Kansas River. Specimens from the southwestern Kansas River drainage (Smoky Hill River) exhibit the low scale indices typical of representatives throughout the remainder of the range.

Whether genetic traits of *E. s. pulchellum* have entered populations east of the Osage-Missouri confluence is uncertain. I think that some of the color-pattern of the western subspecies (dark vertical bars that meet ventrally in breeding males, weakly developed horizontal lines, and predominantly red spinous dorsal fin) has been incorporated in populations of *E. s. spectabile* in tributaries of the Mississippi River in Missouri and Illinois and to a lesser degree in tributaries of the Ohio River in Illinois, Indiana, Ohio, and Kentucky exclusive of Cumberland, Green, and Tennessee rivers.

With the exception of Kansas River, where intergrades are responsible for most heterogeneity, the Arkansas River System has the most variation in populations of orangethroats of any river of the plains. *E. s. pulchellum* can be separated into three populations in the Arkansas Basin: (1) Populations west of the Neosho-Verdigris rivers are typical of the plains subspecies from

Nebraska to Texas; males have 10 or fewer vertical bars, are predominantly blue, have transparent, rarely pale yellow, caudal and pectoral fin-membranes, and have no red in the anal fin; (2) Those from the Neosho-Verdigris exclusive of tributaries draining the Springfield Plateau (range of *E. s. squamosum*) have 10 or more vertical bars, also are predominantly blue, but have pale yellow membranes in caudal and pectoral fins, and occasionally have red in the anal fin; (3) Those of the eastern Arkansas River from about Fort Smith to Little Rock, Arkansas, have fewer than 10 vertical bars, are predominantly reddish orange, have transparent, rarely pale yellow, membranes in caudal and pectoral fins, and rarely possess red in the anal fin. In the third region, breeding males are as deeply barred with blue or blue-green as in *pulchellum* elsewhere, but reddish orange pigment is more extensive on interspaces, anterior sides, and belly; the belly, rather than having one or two isolated, oblong, red blotches, as in *E. s. spectabile*, is colored by extension of reddish orange from sides of the body. The general post-breeding color is orange; blues fade and leave only underlying melanin. Meristically there is a small increase in the cheek- and nape-scale index, and a one-scale decrease in mean number of pored scales. Orangethroats in some southern tributaries (Poteau, Fourche La Fave, and Petit Jean rivers) are smaller than specimens from other parts of the range of *pulchellum*. Breeding males average 30 mm in standard length against an average of about 40 mm elsewhere. In other features, they differ little from populations in the remainder of the drainage. Tributaries in which the small orangethroats were collected drain the north slope of the Ouachita Mountains and seemed (at the time of collecting) to be intermittent in flow. The small size of specimens may be due to low productivity of the region (lack of limestones) and/or high mortality-rates in older age-classes when tributaries are dry.

Throughout the Arkansas Basin the anal and pelvic fins of breeding males are strongly tuberculate and many males have tuberculate ventral scales. A narrow, green or blue-green suprabasal band usually is present in the spinous dorsal fin from this drainage southward into Texas. Anal fin-rays average 6.6 west of the Poteau River and 6.3 east.

Occurrences of the orangethroat in the Red River are limited generally to its northern tributaries, from the Wichita and Arbuckle mountains eastward to Little River Drainage of southeastern Oklahoma. The only locality record for a southern tributary of Red River seems to be Rock Creek, Cook County, Texas (Riggs and Bonn, 1959). The greatest amount of variation in this drainage occurs in Blue River, where specimens are snub-nosed, deep-bodied, and have extensive red in the anal fin. The Blue River population represents a hybrid swarm between *E. radiosum cyanorum* Moore and Rigney and *E. s. pulchellum* (see Natural Hybridization). The easternmost collection from the Red River Basin I examined was taken from Mountain Fork River, a tributary of Little River, McCurtain County, Oklahoma.

Seven of nine specimens have one to several scales on the opercle (mean anterior index 0.7), all have a complete supratemporal canal, and the number of posterior infraorbital pores varies from one to four. Unlike the Blue River hybrids, the general body shape is that of *pulchellum*. The above characters may suggest introgression with a related darter (*E. asprigene* or *E. radiosum*), but a more thorough study of this region is necessary before the variation found here is explicable.

Though variation of scale size and minor variation in color exists among populations in the Brazos, Colorado, and Guadalupe river systems in Texas, all orangethroats there are representatives of the plains subspecies.

PRIMARY LITERATURE RECORDS AND MISIDENTIFICATIONS. This subspecies has been reported under the following names:

Oligocephalus pulchellus Girard (1859b) original description—Collette and Knapp (1967) catalog of type specimens. *Astatichthys pulchellus*—Vaillant (1873) in part, description, figure, incorrect type locality "Indiana River." *Poecilichthys lepidus*—Jordan and Gilbert (1882) in part, synoymy by implication in footnote; Ortenburger and Hubbs (1927) Oklahoma. *Poecilichthys coeruleus* (Storer)—Gilbert (1884) Ellis Co., Kansas. *Etheostoma variatum* Kirtland—Gilbert (1885b) Ellis Co., Kansas; Cragin (1885) Ellis Co., Kansas. *Etheostoma varietum spectabile*—Graham (1885) Kansas River. *Etheostoma coeruleum*—Evermann and Fordice (1886) Timber Creek, Winfield, Kansas. *Etheostoma lepidum*—Jordan and Gilbert (1886) characters, Brazos River, Texas; Hay (1887) northwestern Kansas; Jordan (1891) Wichita, Kansas; Meek (1895) Arkansas River, Arkansas; Evermann and Cox (1896) Kansas River; Meek (1896) in part, Arkansas, Oklahoma, and Texas; Jordan and Evermann (1896) in part, synonymy, characters, distribution. *Etheostoma caeruleum lepidum*—Gilbert (1886) characters, Kansas; Gilbert (1889b) Poteau River, Arkansas; Meek (1894) Waldron, Arkansas. *Etheostoma coeruleum spectabile*—Evermann and Cox (1896) Kansas River basin. *Etheostoma arcus-celestis*—Crevecoeur (1903) original description. *Etheostoma arcuscelestis*—Crevecoeur (1908) Mound Creek a tributary of Vermillion River, Onaga, Kansas. *Oligocephalus coeruleus lepidus*—Jordan (1929) in part, characters, distribution. *Poecilichthys coeruleus pulchellus*—Hubbs and Ortenburger (1929) characters, distribution, systematics. *Oligocephalus lepidus*—Jordan, Evermann, and Clark (1930) in part, check list. *Poecilichthys spectabilis pulchellus*—Breukelman (1940) distribution, northwestern Kansas; Jennings (1942) Blue River, Kansas; Cross and Moore (1942) Poteau River of Arkansas and Oklahoma; Simon (1946) provisionally included in Wyoming; Baughman (1950) Texas; Bailey (1948) characters. *Boleichthys fusiformes* (Girard)—Breukelman (1940) inferred reference to *pulchellum*, Logan and Scott Cos., Kansas. *Poecilichthys spectabilis*—Moore and Cross (1950) comparison to *P. jessiae;* Moore and Rigney (1952) southeastern Oklahoma. *Etheostoma spectabile pulchellum*—Bailey (1951) possible occurrence in Iowa; Beckman (1952) characters, Colorado; Knapp (1953) Texas; Cross (1954) Cottonwood River, Kansas; Bailey and Goshne (1955) vertebral counts; Bailey (1956) possible occurrence in Iowa; Schelske (1957) Fall and Verdigris rivers, Kansas; Metcalf (1959) Caney, Walnut, and Elk rivers, Kansas; Minckley (1959) Blue River, Kansas; Deacon and Metcalf (1961) Wakarusa River, Kansas; Collette (1965) breeding tubercles; Metcalf (1966) Kansas River System; Collette and Knapp (1967) catalog. *Etheostoma spectabile*—Moore (1952) Oklahoma; Jurgens and Hubbs (1953) Texas; Hubbs, Kuehne, and Ball (1953) Guadalupe River, Texas; Hubbs (1954) distribution, Texas; Linder (1955a) Verdigris River, Oklahoma; Linder (1955b) Blue River, Oklahoma; Kuehne (1955) Guadalupe and San Antonio rivers, Texas; Moore and Buck (1955) Chikaskia River, Kansas; Strawn (1955) Colorado and Guadalupe rivers, Texas, behavior; Minckley (1956) Deep Creek, Riley Co., Kansas; Strawn and Hubbs (1956) stripping; Hubbs (1957a) check list, Texas; Hubbs (1957b) distribution patterns, Texas; Hubbs (1957c) sperm viability; Hubbs and Strawn (1957a) hybrid survival; Hubbs and Strawn (1957b) hybrid variability; Clark, Breukelman, and Andrews (1958) Lyon Co., Kansas; Hubbs (1958a) hybrid fertility; Linder (1958) behavior, hybrids; Hubbs (1958b) variation in egg complement; Minckley and Cross (1959) Kansas River Basin; Hubbs (1959) hybrid combinations; Riggs and Bonn (1959) Red River, Oklahoma and Texas; Hubbs and Hettler (1959) Colorado River, Texas, ecology; Blair (1959) northeastern Oklahoma; Hubbs, Littlejohn, and Littlejohn (1960) survival of young; Hubbs and Delco (1960) egg size; Hubbs (1960) functional duration of sperm; Hubbs (1961a) temperature tolerance; Hubbs (1961b) gamete compatibility; Hubbs and Laritz (1961) natural intergeneric hybrid;

Deacon (1961) Neosho River, Kansas; Strawn (1961) meristic variation; Hubbs and Armstrong (1962) temperature tolerance; Jones, Hettler, and Hubbs (1962) egg survival; Hubbs and Strawn (1963) temperature tolerance; Metcalf (1966) Kansas River System. Cross (1967) characters, habits, distribution in Kansas; Summerfelt (1967) Smoky Hill River, Kansas.

Etheostoma spectabile squamosum subsp. nov.

Arkansas River Scaly Orangethroat

Figure 1A

Type. Holotype (KU 7476) an adult male 45.4 mm in standard length, collected by D. A. Distler and B. A. Simco, April 23, 1961, in Indian Creek, a tributary of Elk River, 2.5 miles southwest of Sweetwater, Newton Co., Missouri, on State Road D. Paratypes are 33 additional specimens (KU 7477) collected with the holotype.

Diagnosis. *E. s. squamosum* differs from other subspecies of *E. spectabile* by having the anterior region moderately scaled (anterior index 2) and coloration resembling that of *E. s. pulchellum* except that horizontal lines are more conspicuous and vertical bars less distinct on upper sides.

Coloration. *Breeding males:* Generally like that of *E. s. pulchellum* but vertical bars most dense on lower sides and across ventrum, especially on caudal peduncle; bars rarely confluent with dorsal saddles. Spinous and soft dorsal fins predominantly orange but with a narrow suprabasal, green band. Often, amorphic blotches of orange on membranes of anal fin, principal rays of caudal fin, and distal margin of pectoral and pelvic fins. Dorsal saddles most prominent at origin of spinous dorsal fin, between spinous and soft dorsal fins, and at posterior end of soft dorsal fin.

Non-breeding males: Chromatic colors subdued or wanting. Faint orange on posterior sides, dorsal fins, and branchiostegal membranes. Faint blue-green on banded area of caudal peduncle.

Females: Often devoid of chromatic colors even at peak of breeding season; occasionally having a pale submarginal band of orange on dorsal fins. Broken horizontal lines more conspicuous than in males.

Additional Characters. Within the range of the subspecies are two major river systems draining the western Ozarks: the lower Grand (Neosho) River (eastern tributaries) and the Illinois River system. Color patterns seem not to differ greatly between the two drainages, but some meristic characters vary both between and within the two systems. The number following the character is the whole number nearest the mean. The range appears in parentheses. *Lateral line scales* (Table 4): 48 (40-56), no significant variation of mean number from headwaters to mouth in either river system but an increase of 1 in mean number from Grand to Illinois river. *Pored lateral line scales* (Table 7): 30 (20-41), variation as above but with an increase of about 2 (29.0-30.8) in mean number from Grand River to Illinois River. *Diagonal scales:* 13 (11-16), modal number 13 throughout range but a small

increase in mean number (13-13.5) from Grand River to Illinois River. *Scales above lateral line:* 6 (5-7), modal number 6 throughout range but increase in mean number (0.3) from Grand River to Illinois River. Anterior squamation (Table 11): Cheek naked to well scaled, usually moderately scaled, mean index 2.2 in Grand River, 1.9 in Illinois River. Opercle naked to well scaled, usually moderately scaled, mean index 2.0 in Grand River, 1.9 in Illinois River. Nape naked to well scaled, usually well scaled, mean index 2.8 in Grand River, 2.8 in Illinois River. Breast naked to well scaled, usually lightly scaled, mean index 1.4 in Grand River, 0.7 in Illinois River. Mean anterior index 2.1 in Grand River, 1.8 in Illinois River. *Posterior infraorbital pores* (Table 15): 3 (2-5), infraorbital canal complete in 2 per cent of individuals from Grand River, 3 per cent from Illinois River. *Supratemporal canal* (Table 15): Usually complete, 11 per cent from Illinois River and 23 per cent from Grand River having incomplete canals. *Gill membranes:* Moderately connected, mean index 2 throughout range. *Lepidotrichs:* Spinous dorsal 10 (8-11); soft dorsal 13 (11-15); anal soft rays 7 (6-8); pectoral 12 (11-13). *Breeding tubercles:* Anal and pelvic lepidotrichs tuberculate; lower pectoral rays sometimes ridged in Elk River (Grand River drainage); pectoral rays and ventral scales tuberculate in headwaters of Illinois River. *Genital papilla of males:* Generally ovate in shape; apex acuminate, obtuse, truncate, or rounded.

RANGE. Southeastern Kansas, southwestern Missouri, northwestern Arkansas, and northeastern Oklahoma in streams draining the Springfield Plateau west and southwest into the Arkansas River.

INTERGRADES. With *E. s. pulchellum* in lower tributaries of Neosho River in southeastern Kansas, in lower tributaries of Spring River near confluence with Neosho (Grand) River, in Illinois River of Oklahoma near confluence with Arkansas River, and in Sallisaw Creek; intergradation may occur with *E. s. spectabile* in headwaters of Illinois River.

DISCUSSION. The range of *E. spectabile squamosum* lies mainly within the Ozark biotic district of Blair and Hubbell (Blair, 1959). Intergrades with *E. s. pulchellum* are found in the northern part of the range near the junction of the Ozark and Cherokee Prairie biotic districts, and in the southern part of their range near the junction of the Ozark and Osage Savanna biotic districts, but mostly within the latter.

Its restriction to a single biotic zone suggests that *squamosum* may be an ecophenotype. However, the characters that distinguish it from the other subspecies are stable in specimens hatched and reared in the laboratory; there is no loss of anterior squamation or changes in the pattern of pigmentation.

Past isolation of populations of *pulchellum*, perhaps as we know it today, in streams draining the Springfield Plateau probably occurred during the extensive pluvial periods of the Pleistocene when the silt- and sand-loaded

Arkansas River was even more a barrier to dispersal than at present. Such populations could have evolved into *squamosum*.

Alternative means of origin of this subspecies exist. *E. spectabile squamosum* may have evolved through introgression with one or more related species. The density of anterior squamation, presence of three well developed dorsal saddles, and high percentage of complete infraorbital canals (when compared with the plains subspecies) suggest introgression with a darter or darters having those characters. *Etheostoma whipplei* (Girard), a related darter, is partly sympatric with *squamosum* and throughout most of its range is sympatric with *E. s. pulchellum*. In the area of sympatry, *E. s. pulchellum* and *E. whipplei* occasionally hybridize when both are compelled to spawn in the same area because of drouth or other adverse conditions. If such hybrids are fertile, however, their progeny usually do not survive in competition with normal offspring, or are swamped by backcrossing with the parental species. Hubbs (1955), in a discussion of hybridization among fishes, suggests that when two related species are sympatric, and one is much more abundant than the other, hybridization is likely. *E. whipplei* is found only rarely in the Ozark biotic districts but is abundant in the Osage Savanna and Cherokee Prairie biotic districts (Blair, 1959, Fig. 4). If hybridization between *E. whipplei* and *squamosum* has occurred, it is reasonable to assume that some of the genome of the less abundant species (*E. whipplei*) has been incorporated into that of the more abundant species because backcrossing would tend to be unidirectional. *E. whipplei*, although possessing some of the characters that distinguish *squamosum* from other subspecies of orangethroats (moderately scaled anterior region, complete infraorbital and supratemporal canals, extensive red in the fins) does not possess the tri-saddle pattern characteristic of *squamosum*.

Another related species is *Etheostoma caeruleum* Storer, the rainbow darter, in which the tri-saddle dorsal pattern does occur. Among the subspecies of *Etheostoma spectabile, squamosum* is unique (except for populations of *E. s. pulchellum*, in the Neosho River) in sharing the tri-saddle pattern with *E. caeruleum*. *E. s. squamosum* also resembles *E. caeruleum* in being moderately scaled anteriorly (but unlike *caeruleum, squamosum* has a moderately to well scaled cheek). Also, *squamosum* resembles *E. caeruleum* in having less red in the fins than does *E. whipplei*.

E. caeruleum, while it is sympatric with most subspecies of *E. spectabile*, it is not so with *squamosum* (and *E. s. pulchellum*) because *E. caeruleum* is not indigenous west of the Ozark Plateaus in tributaries of the Arkansas River. However, *E. caeruleum* is abundant in tributaries of White River immediately adjacent to the area drained by the Illinois and Grand rivers of southwestern Missouri and northwestern Arkansas, where *squamosum* occurs.

The divides between the Arkansas and White river drainages are narrow

and there is evidence that these have been crossed by various aquatic organisms during the Pleistocene (Williams, 1954; Branson, 1963). Moreover, Branson (1963) states that "... it would appear that the Neosho has captured the Spring River-Shoal Creek System, and possibly the Elk River as well, from the White River Drainage." Bretz (1965), however, in a study of the geomorphic history of the Missouri Ozarks, indicates that there is a lack of geologic evidence for stream piracy across the Springfield Plateau and that "... the more favored streams of the steeper eastern slope have captured nothing more from the western slope than additional runoff areas."

Also in northwestern Arkansas, the surfaces of the divides, which are narrow between the Illinois and White rivers (Quinn, 1958), may not be a barrier to small aquatic organisms. Both of these streams drain the Springfield Plateau. Western drainage is effected by tributaries of the Illinois River and eastern drainage by tributaries of White River. The Springfield Plateau is underlain by cherty limestone of Mississippian age; however, much of the limestone has weathered away, leaving a porous mantle of resistant chert up to 150 feet in thickness in the uplands (Thornbury, 1965). This porous mantle accounts for reduced surface runoff of the region and rapid diversion of surface water to the subsurface where it then emerges as springs or seeps usually at the level of the water table. A combination of narrow divides and extremely porous substrate suggests to me that the barriers for small aquatic organisms are lower in elevation than the surface of the divides of the dissected plateau. The bedrock underlying the chert perhaps serves as an effective divide during all but pluvial periods when these subsurface divides are breached by water both above (vadose) and at level of the water table (phreatic). Indirect evidence of such phenomena was brought to my attention while I was collecting fish in northwestern Arkansas (western drainage of the Springfield Plateau). A resident informed me that a large spring on his property became muddy periodically after heavy rains in the White River watershed just across the divide. Emphasis was made that no rain had fallen on his (Illinois River) side of the divide. This suggests to me that not only was his spring sustained by ground water from the Illinois River watershed, but that the spring was also connected, if only periodically, to surface drainage and vadose water across the divide (White River watershed).

An adult male rainbow darter *(E. caeruleum)* was collected from the headwaters of the Illinois River near Savoy, Washington County, Arkansas, by members of an ichthyology class at the University of Arkansas. To my knowledge, this is the first record of the rainbow darter from Arkansas River drainage, although it is abundant in tributaries of White River. The specimen collected from the Illinois River was in peak breeding condition and if it spawned, it probably did so with females of *E. spectabile squamosum*. Several hundred specimens of *squamosum* were collected with the single

specimen of the rainbow darter. The latter, of course, could have arrived in a bait bucket. Introduction, by this or by natural means, of an occasional specimen or small numbers of *E. caeruleum* into the range of *squamosum* would enhance the chance of unidirectional hybridization. Although back crossing (again unidirectional) would tend to swamp most characters of the least abundant species, some characters might in time become incorporated into the population. The characters which *squamosum* shares with *E. caeruleum* seem to me to be sufficiently constant so that their acquisition is unlikely to date from a time after the arrival of Caucasian man.

In general the orangethroat is less streamlined in shape than either *E. caeruleum* or *E. whipplei* and seems to prefer less swift currents than the latter two species. *E. spectabile squamosum*, on the contrary, is found in currents as strong as those preferred by *E. caeruleum*, particularly in the Elk and Illinois rivers. In these drainages, *squamosum* occupies habitats equivalent to those of *E. caeruleum* and possibly also *E. whipplei*.

Natural selection alone or natural selection and introgression of the genome of *E. whipplei* and/or *E. caeruleum* with the plains orangethroat may be responsible for the evolution of *squamosum* in western drainages of the Springfield Plateau. Continuous unidirectional hybridization is possible considering the distribution of these darters.

Primary Literature Records and Misidentifications. This subspecies has been reported under the following names:

Etheostoma caeruleum Storer—Gilbert(1889a) characters, northeastern Oklahoma. *Etheostoma coeruleum spectabile* (Agassiz)—Meek (1891) Shoal Creek, southwestern Missouri; Meek (1894) Illinois River at Prairie Grove, Arkansas; Meek (1895) tributaries of Arkansas River in northwestern Arkansas. *Poecilichthys coeruleus: pulchellus* × *spectabilis*—Hubbs and Ortenburger (1929) characters, distribution in northeastern Oklahoma. *Poecilichthys spectabilis* —Moore and Paden (1950) Illinois River in Oklahoma. *Etheostoma spectabile*—Hall (1952) northeastern Oklahoma: Moore (1952) Oklahoma; Blair (1959) distribution in northeastern Oklahoma; Cross (1967) scale characters, Spring River, Kansas.

KEY TO THE SUBSPECIES OF *ETHEOSTOMA SPECTABILE*

This key is based on the coloration and anterior squamation of breeding males. For a comparison of subspecies based on characters other than coloration, see Table 1.

A. Orange prevalent color of dorsal fins, suprabasal blue band of spinous dorsal thin and incomplete or absent. Blue usually absent from sides of head ..... B.

B. Transverse bars of melanin usually of equal density on upper and lower sides; horizontal lines discontinuous and indistinct, mostly evident near lateral line and several scale rows below; dorsal saddles usually of equal density; suprabasal band of spinous dorsal fin usually absent; head usually naked. ..... *E. s. pulchellum*

BB. Transverse bars of melanin of unequal density on upper and lower sides, less dense or lacking on upper sides; horizontal lines more continuous and distinct than above, developed on upper and lower

sides; dorsal saddles of unequal density (cranial, midpterygial, and caudal saddles most dense); suprabasal blue band of spinous dorsal fin usually lightly developed; head scaly. ..... *E. s. squamosum*

AA. Blue prevalent color of dorsal fins or blue and orange equal in area of development. Blue variably present on sides of head (often absent east of Mississippi River). ..... C.

C. Transverse bars of equal density from axilla to caudal base; humeral spot small but distinct; belly white, blue-gray, or rusty, usually barred by extension of melanin from sides; genital papilla without chromatic colors, immaculate or lightly stippled with fine melanophores. ..... D.

D. Transverse bars dense, often forward-slanting; suprabasal blue band of spinous dorsal fin wider than submarginal orange band; cheek blue, rarely well scaled; genital papilla immaculate, occasionally having a single submarginal row of fine melanophores. ..... *E. s. uniporum*

DD. Transverse bars of melanin faint, usually subvertical; submarginal orange band of spinous dorsal fin wider than suprabasal blue band; cheek cream-colored, usually well scaled. ..... *E. s. fragi*

CC. Transverse bars most dense on posterior sides, often subtriangular on caudal peduncle; humeral spot indistinct or wanting; belly with two oblong, orange patches on each side of midline or with patches confluent, uninterrupted by crossbars; genital papilla often blue-gray, saturated with fine melanophores. ..... *E. s. spectabile*

ZOOGEOGRAPHY

No fossil remains of *E. spectabile* are known. The evolutionary history of the species can be surmised only from its present distribution, what is known of the history of changes in drainage throughout the range, and the present location and characteristics of geographic variants.

Preglacial and Glacial Drainage

The history of drainage as presented herein rests variously upon the evidence and arguments presented by: Bayne and Fent, 1963; Bretz, 1965; Fenneman, 1938; Flint, 1961; Frye and Leonard, 1952, 1963; Heim and Howe, 1963; Lueninghoener, 1947; Lugn, 1935; Quinn, 1957, 1958; Seevers and Jungmann, 1963; Stricklin, 1961; Thornbury, 1965; Ver Stegg, 1946; and Wayne, 1952.

Knowledge of late Tertiary drainage is incomplete, especially in the western part of the present range of the species, but there seems to be sufficient geologic evidence to make reasonably clear the major history of drainage.

In the late Pliocene, at least two south-flowing drainages existed between the Rocky Mountain System and Appalachian Highlands. A minor western river system (Ancestral Plains Stream System of Metcalf, 1966) drained

much of the southern one-half of the Great Plains Province, and a major eastern river system (Teays-Mississippi) drained the lower one-half of the northern Great Plains, the southern Central Lowlands, the Interior Low Plateaus, the southwestern Appalachian Plateaus, and the Ozark Plateaus. At present there is insufficient geologic evidence to ascertain whether the Ancestral Plains System flowed directly into the Gulf of Mexico or joined the Teays-Mississippi via the preglacial Arkansas River or Red River.

During the Pleistocene, multiple glaciation, changes in stream regimen, and regional tilting altered Tertiary drainage considerably to form the present Mississippi River System.

Western Region. Nebraskan ice had little effect on the Ancestral Plains System. Valleys were deepened, but drainage was still southward.

Kansan ice initiated changes in drainage that continued throughout the epoch. According to Frye and Leonard (1952), the southwestern lobe of this glacier overrode the Flint Hills upland in what is now northeastern Kansas. This upland formed a divide between the Ancestral Plains and the Teays-Mississippi river systems. Meltwaters from south of the lobe and east of the divide flowed eastward along the Wakarusa Valley into the Teays-Mississippi system. Meltwaters from the western edge of the glacier and west of the divide flowed southwestward into the Ancestral Plains system, greatly increasing its watershed (Frye and Leonard, 1952, Fig. 13). In early Yarmouth time the enlarged Plains drainage was partially beheaded by tributaries of the developing Mississippi River; plains drainage from the Saline River of Kansas northward flowed east via the Missouri River Valley.

By (or during) Illinoian time the Ancestral Plains System seems to have been altered further. According to Quinn (1958) the ancestral lower Arkansas River breached the divide near Magazine Mountain in Arkansas and captured a large part of the Ancestral Plains System to form the present Arkansas River Basin. To the south, a tributary of the Brazos shifted its course westward and was captured by the Red River (Stricklin, 1961). To the north, the Smoky Hill River was captured by a tributary of the Kansas River by late Illinoian or early Wisconsin time.

Little information is available concerning Pleistocene drainage between the present Red and Arkansas rivers and in the region south of the Brazos. Frye and Leonard (1952) describe a minor southward flowing drainage in southwestern Kansas that was present in late Nebraskan time; much of this drainage was aggraded during Kansan time and the remainder was integrated into the Arkansas River. Whether this drainage originally flowed into the Red River is unknown, but I judge that this or some other southern tributary of the present Arkansas River flowed south into the valley of Red River prior to its capture by the Arkansas River. Quinn (1957) describes the region of central Texas in Nebraskan time as a surface of little relief and considerable elevation. During the following glacial periods this area

was alternately degraded and aggraded by the action of streams. During Sangamon time, valleys below the Balcones Escarpment were filled completely with gravel. This fact suggests to me that divides between these valleys were breached by the waters that carried this gravel; hence, faunal interchange may have occurred between such rivers as the Brazos and Colorado and between the Colorado and Guadalupe below the Balcones Escarpment.

EASTERN REGION. Thornbury (1965) illustrates and discusses various interpretations of the Teays-Mississippi preglacial and glacial drainage. The major features that could have influenced dispersal of the orangethroat are as follows. The preglacial Mississippi River was joined by the Teays River in what is now central Illinois, and flowed southward along the present Illinois River Valley. Instead of meeting the Ohio River at the present confluence (Cairo, Illinois), the Mississippi River turned southwestward and flowed along the edge of the Salem Plateau in a valley near that now occupied by Black River and lower White River. The preglacial Ohio River probably originated near the present site of Madison, Indiana, and flowed southwestward along much of its present course; but, south of Golconda, Illinois, the river flowed westward through the Cache Lowland to Cape Girardeau, Missouri, then southwestward along the eastern edge of Crowley's Ridge (present St. Francis Basin), and united with the Mississippi River either below present Helena, Arkansas, or farther south near Simmesport, Louisiana. An alternate interpretation is that the preglacial Ohio originated east of present Cincinnati, Ohio, and included as tributaries the Kentucky, Licking, and Miami rivers; in the former interpretation, these rivers were part of the Teays Drainage. Opinions differ as to the preglacial course of the Tennessee River. It and the Cumberland River may have united with the Ohio before flowing through the Cache Lowland, or may have followed a course south of this lowland (along the western edge of the Interior Low Plateaus Province) before uniting with the Ohio River southeast of Crowley's Ridge.

Drainage changes in the Teays-Mississippi System were initiated by Nebraskan ice. The lower Teays was blocked and the upper course ponded until waters spilled over low divides into the Ohio River. Not until late Kansan time, however, was the present drainage of the Ohio River established by integration of former Teays and Lake Erie drainage. Illinoian ice continued to aggrade valleys and divert water to the developing Ohio River. By late Illinoian or early Wisconsin time the channel of the Mississippi River shifted eastward from the Salem Plateau to a lower level, through several gaps in Crowley's Ridge, and joined the Ohio on the eastern flank of this highland. Wisconsin ice aggraded most of the remaining Teays and lower Mississippi valley with sediment from the region of glacial Lake Agassiz and the Great Lakes. Changes following Wisconsin glaciation are evident

in the present drainage. The major changes were shift of the upper Mississippi River westward from the Illinois River Valley, diversion of the Ohio River southward from the Cache Lowland to unite with the Tennessee River near Paducah, Kentucky, a further shift eastward of the lower Mississippi River to its present channel, and loss of Great Lakes drainage to the Mississippi River System, culminating in the present Mississippi Basin.

Origin and Disperal

The orangethroat darter may have originated in one of the following regions; north of the Teays-Mississippi (Hudson Bay), upper Mississippi, Teays, eastern drainage of the lower Mississippi (Interior Low Plateaus), or western drainage of the lower Mississippi (Ozark Plateaus). The least likely centers of origin will be discussed first.

If the orangethroat darter originated north of the Teays-Mississippi System, no evidence to that effect remains; the species is absent from the northern drainage that was not affected by glaciation (upper Missouri River). No evidence would be expected from the St. Lawrence System because this region was heavily glaciated. Populations present in the western Lake Erie drainage probably arrived via post-glacial routes. Specimens in this region resemble those in the Wabash River of Indiana, indicating that they entered the Lake Erie Basin in late Wisconsin time or subsequently via the glacial Lake Maumee outlet. Gerking (1945) indicated that the divide between the upper Wabash and Lake Erie is low, and that connections across this divide were observed during a period of high water in 1914. Perhaps this low divide had been crossed frequently by orangethroats during pluvial conditions.

Either the preglacial Teays or upper Mississippi may have been the center of origin, but here again the evidence is weak. Orangethroats are absent from the Driftless Area of Wisconsin and populations now present in the Platte River could have arrived there as late as mid-Pleistocene. The species is present in the Kentucky, Licking, Miami, and Scioto rivers (presumably all tributaries of the preglacial Teays), but absent in eastern tributaries of the Teays having suitable habitat (Muskingum, Sandy, and Kanawha rivers.) If the orangethroat or its oligocephalid ancestor occurred or originated in the Teays or upper Mississippi, Pleistocene glaciation would have forced populations into southern refugia in the Ozark and Interior Low plateaus where secondary centers of dispersal developed.

Evidence for origin in the preglacial Ohio (Wabash through Tennessee rivers) is somewhat stronger than for origin in the above regions. The occurrence of endemic populations in the lower Green (Barren River), Cumberland, and Tennessee rivers suggests that the orangethroat occupied this region throughout much of the Pleistocene. Dispersal westward into the

Ozarks may have occurred early in the epoch before the course of the Mississippi shifted eastward from the Ozark highlands.

I think that the most likely center of origin lies in the Ozark Plateaus. The greatest amount of racial diversity occurs in that region. From there, also, preglacial pathways of dispersal extended east, north, and westward into the Teays-Mississippi and probably westward into the Ancestral Plains system. The cold, torrential waters of the Mississippi would have isolated populations of orangethroats in the southeastern Ozarks during Nebraskan time. By late Nebraskan or early Aftonian time, however, populations could have dispersed northward into the developing Mississippi River System via the mainstream along the eastern edge of the highland and/or across divides (discussed by Bretz, 1965) between the White and Missouri rivers. Later, Kansan glacial ice doubtless isolated populations in the northern Salem and Interior Low plateaus, and the Mississippi again isolated populations in the southeastern Ozarks. By late Kansan or early Yarmouth time, the course of the lower Mississippi shifted eastward, leaving an alluvial plain as a barrier to further dispersal from the southeastern Ozarks. Illinoian ice, which achieved the greatest southward advance in the east, probably had the greatest effect east of the Mississippi River, again isolating populations in southern tributaries of the developing Ohio River as well as separating them from populations in the Ozarks. By late Illinoian or early Sangamon time, the course of the lower Mississippi shifted east of Crowley's Ridge leaving a still wider alluvial plain. Populations of orangethroats in the Missouri and Ohio rivers dispersed northward as sufficient habitat became available. Meltwaters of the Wisconsin glacier (which underwent a series of four to six advances and retreats) again probably separated eastern and western populations, but doubtless did nor force populations in the Ohio so far southward as the previous glacier had done, thus allowing for dispersal northward into the south-flowing tributaries of the Ohio River.

Etheostoma spectabile may have dispersed into the Missouri-Platte System in early Pleistocene and then have been isolated by either Nebraskan or Kansan ice in the Platte, where it evolved into *E. s. pulchellum;* southward dispersal over the Plains could have occurred from late Kansan to early Sangamon time. The similarity of now disjunct populations of *pulchellum* suggests that these populations have not been isolated from each other long. The subspecies *pulchellum* must have evolved from Teays-Mississippi stock no later than Kansan time to take advantage of routes of dispersal through the Ancestral Plains System available to it in late Kansan and early Yarmouth time. When the Kansas River captured a portion of the Ancestral Plains System, it not only isolated certain populations of *E. s. pulchellum* from others farther south, but it also brought the plains subspecies in contact with populations of *E. s. spectabile* of the Kansas-Missouri System. Evidence of intergradation between *pulchellum* and *spectabile* at

present occurs in some specimens from the Platte-Republican rivers and becomes progressively more common eastward in the Kansas and Missouri rivers. Lack of intergradation in the Smoky Hill River seems to reinforce evidence for the late capture of this stream by the Kansas River (late Illinoian or early Wisconsin).

Other possible interpretations for the origin of *pulchellum* are that it evolved from stock autochthonous in tributaries of the upper White River (in Missouri and Arkansas) that were pirated by the Arkansas River (Spring-Neosho) in the early Pleistocene. According to Bretz (1965), there is little geologic evidence of headwater exchange between the Arkansas and White rivers in Missouri. However, Williams (1954), in discussing the distribution of the crayfish *Orconectes neglectus* (Faxon), suggests that this species dispersed from the Ozarkian center of origin (White River) across divides into the Spring-Neosho System and northward through the Plains to the Platte River via the Pleistocene stream connections proposed by Frye and Leonard (1952). If such a capture did occur, it would suggest that the orangethroats now found on the west side of the Springfield Plateau (*squamosum*) descended from, or their ancestors gave rise to, "pro"-*pulchellum* stock.

Alternatively, *pulchellum* may have evolved from Teays-Mississippi stock isolated in highland tributaries of the lower Arkansas River Valley (drainage of the Ouachita and Boston mountains) by meltwaters of the Nebraskan glacier. However, evidence for dispersal of Teays-Mississippi stock to this region is weak. Although *pulchellum* occurs in this region at present as a population having color patterns distinct from those in the remainder of the range (suggesting some isolation), no orangethroats have been found in tributaries of Little Red River which drain the southeastern Ozarks between the valleys of the Arkansas and White rivers. The failure of "pro"-*pulchellum* to reach the Little Red and Arkansas rivers from the White River via the Mississippi River may perhaps be explained by lowland barriers to dispersal in the preglacial Mississippi Valley (see Thornbury, 1965, Fig. 3.17). Near its confluence with the White River, the course of the preglacial Mississippi turned eastward away from the Ozark highland and flowed in an alluvial valley more than 50 miles east of where the Arkansas River cuts into the highland. The course of the preglacial Arkansas River did not join the Mississippi River at this point, however, but flowed southward parallel to the course of the Mississippi before joining it more than 170 miles south of their present confluence. Assuming the Mississippi Alluvial Plain and the western Gulf Coastal Plain were as much a barrier to dispersal then as they are today, it is unlikely that *E. spectabile* invaded streams draining the Ozark and Ouachita provinces south of White River via these alluvial valleys. The western subspecies probably invaded the eastern Arkansas River Basin (Fort Scott to Little Rock, Arkansas) from a more western center (Ancestral Plains System).

NATURAL HYBRIDIZATION

Hybridization between *Etheostoma spectabile* and other species is not common, but has been reported with *E. radiosum* (Hubbs and Black) and *E. whipplei* (Girard) by Linder (1955b), with *E. caeruleum* (Storer) by Knapp (per. comm.), and with *Percina sciera* (Swain) by Hubbs and Strawn (1957) and Hubbs and Laritz (1961).

I have examined specimens that seem to be hybrids from one locality in Kansas (with *E. whipplei*) and two localities in Kentucky (with *E. caeruleum*).

Hubbs (1955) suggests several conditions or circumstances that are conducive to hybridization in nature. Particularly applicable to darters having similar breeding habits are: (1) disturbance of the habitat causing the two species to breed in a habitat intermediate to that preferred by each, (2) one species, for lack of adequate spawning sites, is forced to spawn in the area of another, (3) abundance of one species and scarcity of another in a spawning area induces individuals of the less numerous species to breed with members of the more numerous one because mates of its own kind are unavailable. Linder (1958) concluded that the latter circumstance was responsible for two hybrid specimens he described in 1955 (*E. radiosum* × *E. spectabile*); *E. radiosum* was much more abundant than *E. spectabile* at the collection site in Blue River, Johnson County, Oklahoma. Linder (1955b) noted that the Blue River orangethroat was unlike *E. s. pulchellum* from northern Oklahoma, and suggested that it might be an undescribed subspecies. I examined the series of orangethroats (UMMZ 163876, 163877, 163878) used by Linder to compare with specimens of *E. radiosum cyanorum* (Moore and Rigney), and concluded that these, as well as the two specimens Linder described as hybrids, are members of a hybrid swarm. I compared Linder's data on color pattern and squamation with similar data from representative *E. s. pulchellum* collected at Turner Falls, Murray County, Oklahoma (KU 5249). Both his two hybrids and specimens of the Blue River orangethroat are intermediate in coloration and scale counts between *E. r. cyanorum* and *E. s. pulchellum*. Scale counts are tabulated below; listed are the means of 20 specimens (10 of each sex) from each group, with exception of Linder's hybrids (one of each sex).

Character	*E. r. cyanorum**	Linder's hybrids*	Blue R. o'throat*	*E. s. pulchellum* (KU 5249)
Total lateral line scales	56	53	53	48
Pored lateral line scales	48	40	38	32
Scales above lateral line	8	7	7	6
Scales below lateral line	12	9	8	7

* Data from Linder (1958).

Variation of orangethroat populations in Blue River has been studied by James B. Campbell, Kansas State College of Pittsburg, and he (per. comm.) concurs that these populations are hybrids between *E. r. cyanorum* and *E. s. pulchellum*.

Perhaps experimental hybridization of *E. r. radiosum* with *E. s. pulchellum* may provide evidence for the origin of *E. r. paludosum* and *E. r. cyanorum*. Possibly both *E. r. paludosum* and *E. r. cyanorum* arose by hybridization with and periodic isolation from populations of *E. s. pulchellum*.

With regard to the hybrid combination *E. whipplei* × *E. s. pulchellum*, Linder (1955b) reported predominance of the orangethroat (82 per cent, of which 61 per cent were females) at the hybrid locality. F. B. Cross (per. comm.) took only one specimen of *E. whipplei* at the locality in Verdigris River where the hybrid (KU 3165) was obtained; *E. s. pulchellum* was abundant at this locality. When the specimens were collected (April 1, 1954), Kansas was in the third year of a severe drouth and most tributaries of the Verdigris River were dry. The collection was made in the mainstream at Altoona, Kansas, on a riffle only a few inches deep.

Hubbs and Laritz (1961) suggest that the natural hybrid *P. sciera* × *E. spectabile* resulted from great abundance of *P. sciera* and scarcity of *E. spectabile* at the locality of capture, and from alteration of the habitat because of extensive collecting.

I am aware of the nature of the habitat at only one location where specimens of *E. caeruleum* × *E. s. spectabile* were collected. The bed of upper Knob Creek in the Salt River Drainage, Bullitt County, Kentucky is composed of a gravel substrate (stones less than egg-size) over which flows a shallow, braided stream. Few fish could be observed in the clear water before collecting, but deep agitation of gravel in the narrow channels yielded an abundance of specimens. The total collection was composed of about 50 per cent *E. s. spectabile*, 40 per cent *E. caeruleum*, and 10 per cent *E. flabellare* Rafinesque. About 10 per cent of the 60 specimens of ostensible *E. s. spectabile* and *E. caeruleum*, I consider to be hybrids between the two. The width of the channel of Knob Creek indicates that the stream often has much greater volume than it did when I seined there. Decreased precipitation seemingly reduced this stream to near-intermittency, forcing several species into similar habitat. Winn (1958b) observed that *E. s. spectabile* and *E. caeruleum* often breed on the same riffle, and have no obvious differences in breeding behavior; nevertheless, Winn never observed interspecific matings under laboratory or field conditions. Winn (1958a) also found that *E. s. spectabile* breeds most often near the heads of small riffles whereas *E. caeruleum* tends to breed in deeper, swifter water at the base of these riffles, and that *E. caeruleum* preferred a coarser substrate than *E. s. spectabile*. I observed, in the laboratory, that males of *E. s. spectabile* and *E. s. pulchellum* will breed readily with females of *E. caeruleum* when no other mates are

available. Males of *E. caeruleum* were not observed breeding with females of *E. spectabile,* even after the females lay half buried in the sand (which generally initiated mounting-response in males). They obviously did breed, however, because hybrids were produced in aquaria containing only male *E. caeruleum* and female *E. spectabile.* Additional hybrids were examined from Bay's Fork, Barren-Green River Drainage, Allen County, Kentucky. Of a mixed collection of 31 ostensible *E. caeruleum* and *E. spectabile,* I consider 29 per cent to be hybrids between the two species.

Intrinsic mechanisms may minimize hybridization under normal environmental conditions. Hubbs (1960) indicates that darter eggs possess a factor that reduces the chance of fertilization by foreign sperm from sympatric populations of related species but not from allopatric populations, and that the duration of sperm function is greatly reduced in a population of darters sympatric to related species. This may partly explain the rarity of natural hybrids between *E. spectabile* and sympatric congeners that have similar reproductive behavior. Mate selection undoubtedly is a strong factor in maintaining the integrity of related, sympatric species.

EXPERIMENTAL BREEDING

When I began work with *E. spectabile,* I knew of no intergrading populations nor sympatric occurrences of recognized subspecies. Breeding experiments were undertaken to test character stability in progeny of intrasubspecific matings, intersubspecific matings, interspecific matings and various backcrosses reared under similar environmental conditions.

Artificial hybridization (stripping) of *E. spectabile* with other darters has been reported by Hubbs (1959) and Hubbs and Strawn (1957a and b); crosses were with *Percina caprodes* (Rafinesque), *Etheostoma lepidum* (Baird and Girard), *E. grahami* (Girard), *E. caeruleum, E. fonticola* (Jordan and Gilbert), *E. whipplei* (Girard), *E. radiosum* (Hubbs and Black), *E. gracile* (Girard), *E. parvipinne* Gilbert and Swain, *E. blennioides* Rafinesque, a hybrid *Etheostoma (spectabile* × *lepidum),* and the centrarchid *Lepomis punctatus.* In addition, Clark Hubbs (per. comm.) has successfully reared hybrids of *E. spectabile* and the following darters: *Percina sciera* (Swain), *P. phoxocephala* (Nelson), *P. shumardi* (Girard), *P. copelandi* (Jordan), *Etheostoma chlorosomum* (Hay), *E. stigmaeum* (Jordan), *E. tetrazona* (Hubbs and Black), *E. euzona* (Hubbs and Black), *E. zonale* (Cope), *E. juliae* Meek, *E. punctulatum* (Agassiz), *E. flabellare* Rafinesque, *E. proeliare* (Hay), and *E. microperca* Jordan and Gilbert. Linder (1958) allowed *E. spectabile* and *E. radiosum* to hybridize under laboratory conditions.

REARING METHODS

About 50 aquaria of 5 to 25 gallon capacity were set up with grade 2

aquarium gravel and sub-gravel filters. Small slabs of limestone and clamshells were added for cover and establishment of territories, and to help maintain hard-water conditions. Dechlorinated tapwater was added and maintained at a depth of 6 to 10 inches. Continuous aeration was provided by a single large compressor which also operated filters. Favorable temperatures, 15° to 21° C., were maintained by means of two 10,000 B.T.U. air conditioners (room-size 20 x 8 x 8 feet). During the first year of experimentation (1959), fishes in spawning condition were brought from streams and placed in the aquaria. Males and females were stocked and allowed to remain for one week. Parental stock was then removed and the sexes separated in 5-gallon aquaria, to be held for other crosses. In subsequent years, procedures were similar except that most of the breeding stock was reared in the laboratory.

Food. The fish were fed living microcrustacea and mosquito larvae. Newly-hatched fry were fed infusoria, brine shrimp, and the smaller instar stages of zooplankton. An abundance of food was available to the fish at all times.

In nature, the aquatic larvae of insects make up the bulk of the diet of the orangethroat. The plankton that I used as food varied in species composition, but copepods usually predominated, giving way to cladocera in the spring and fall. Deficiency of carotenoids discussed by Hubbs and Stravenhagen (1958) was not apparent in my fish. Darters kept on this diet for three years produced viable offspring, without apparent defects, each year.

Reproduction. In the laboratory, the peak of breeding occurred in late March, April, and May which is the approximate peak in nature at this latitude. Small hatches occurred in aquaria in September, and the earliest hatches occurred in January. Most females seemed spent by early June, but males continued to produce sperm through most of the year (based on microscopic examination of gonad smears). However, the intense colors of males began to fade in late May or early June. During the first winter (1959-60) temperatures in the aquaria were allowed to drop near the freezing point. Colors of males began to deepen and females developed large eggs in December. Darters maintained at 12° C. were not observed to spawn. Spawning was observed when temperatures rose to 15° or 16° C. and the greatest spawning activity seemed to occur between 16° and 20° C.

Growth. Fry were observed usually within two days after adults were removed. As the young fish grew, the brood-tanks were thinned at intervals of several weeks in an attempt to prevent stunting from overcrowding. Only 12 to 14 fish could be raised to sexual maturity in 10 to 12 months in a 25 gallon aquarium (432 sq. in. of substrate), and 3 or 4 darters in a 5 gallon aquarium (108 sq. in. in bottom-area). The number of individuals could be increased about 50 per cent if the water was filtered every 3 or 4 weeks, using a motor-driven charcoal filter. Fish hatched in the laboratory grew more

slowly than those hatched in nature—possibly because of dietary deficiency, lower developmental temperatures, crowding and accumulation of metabolic wastes, or a combination of these factors.

PARASITES. *Hydra* sp. was often introduced into aquaria with food; when abundant, *Hydra* could deplete a tank of fry in less than one week. In tanks of older fishes, *Hydra* consumed enough crustaceans to make it difficult to maintain a sufficient food supply for the darters. This coelenterate was easily controlled by adding 0.05 ml of a saturated solution of copper sulfate per gallon of aquarium water. The only important parasite was the crustacean *Mesocyclops edax*. This copepod seemed harmless in small numbers, and was utilized as food. When abundant, usually in late fall, it often attached to the epidermis of fishes of any size. The reactions of fish to heavy infections of this organism were fast erratic swimming and rubbing against the sides and bottom of the aquarium. When dead or dying fish were removed to a watch glass for observation under magnification, *Mesocyclops* poured off the fish into the water. Copepods tended to leave the host when fish were netted and placed in clean aquaria. Little mortality occurred among infected fish handled in the manner above. Fish allowed to remain in tanks containing large populations of *Mesocyclops* succumbed rapidly to these parasites. True parasitic lernaeid copepods were observed attached to darters in the wild, but no infected individuals were used as brood stock.

RESULTS

E. s. pulchellum

PARENTAL STOCK. Five males and 10 females from Kansas, Douglas Co., Deer Creek, a tributary of the Wakarusa River, T. 12 S, R. 8 E, Sec. 31 were used. All members of this population had the normal color pattern of *pulchellum*. One member of each sex had a few opercular scales.

F_1 GENERATION. All of 117 specimens possessed the normal color pattern of *pulchellum* and had the opercle free of scales. Four males and five females were used for parental stock of the second filial generation.

F_2 GENERATION. All of the 91 specimens had the normal color pattern of *pulchellum* and the opercle free of scales.

E. s. spectabile

PARENTAL STOCK. Two males and 11 females from Kansas, Franklin Co., Hickory Creek, a tributary of the Marais des Cygnes River, T. 16 S, R. 21 E, Sec. 29 were used. All had the normal color pattern of *spectabile* from the Osage River. The opercle was moderately to well scaled, index 2.7.

F_1 GENERATION. Only 24 specimens were reared from this hatch; I overlooked a small adult when the breeding stock was removed, and it probably consumed most of the young. The remaining 13 males and 11 females had the normal color pattern of *spectabile*. The opercle was naked to well scaled,

having an index of 2.6. The same 24 specimens were used as parental stock of the second filial generation.

F_2 Generation. All of 78 specimens had the normal color pattern of *spectabile* and the opercle sparsely to well scaled, index 2.7.

E. s. pulchellum ♂ × E. s. spectabile ♀

Parental Stock. Five males from the *pulchellum* × *pulchellum* cross and 19 females from Hickory Creek were used. One male *pulchellum* had the opercle sparsely scaled. The opercle of females was lightly to well scaled (index 2.8). Each sex had the color pattern normal to its subspecies.

F_1 Generation. Most of the 110 specimens had body color patterns intermediate between *pulchellum* and *spectabile*, with sides tesselated; specimens smaller than 22 mm in standard length usually resembled *pulchellum* in coloration. The first dorsal fin was banded like that of *spectabile*. The opercle was naked to well scaled, usually sparsely scaled, index 1.1. Three members of each sex were used as parental stock of the second filial generation; the opercle of these was sparsely scaled (in two males and two females) to moderately scaled (in one male and one female).

F_2 Generation. Of 49 specimens reared, 15 resembled *spectabile* more than *pulchellum*, 18 were intermediate, and 14 resembled *pulchellum* more than *spectabile* in color pattern of the body. The opercle was naked to well scaled, index 1.3. In 31 specimens, one or both pelvic fins were abnormally developed. Fin-rays were either distorted, short or absent.

E. s. spectabile ♂ × E. s. pulchellum ♀

Parental Stock. Four males from the Hickory Creek collection and 9 females from the *pulchellum* × *pulchellum* cross were used. Three males had the opercle well scaled and one had it moderately scaled. One female had the opercle sparsely scaled, but the remaining eight had naked opercles. Both sexes had color patterns normal for their subspecies.

F_1 Generation. Most of the 88 specimens had body-color patterns intermediate between *pulchellum* and *spectabile;* the sides were tesselated as in the reciprocal cross, and the first dorsal fin was banded like that of *spectabile*. The opercle was sparsely to well scaled usually sparsely scaled, index 1.3 (1.5 in the largest specimens). The squamation differed from that in the reciprocal cross in that the scales were usually embedded in the flesh of the opercle and were difficult to locate in small specimens. Eight males and 10 females were used as parental stock of the second filial generation. The opercle-scale index of this breeding population was 1.6.

F_2 Generation. Of 49 specimens reared, 18 resembled *spectabile*, 26 were intermediate, and 5 resembled pulchellum in color pattern of the body. The opercle was naked to well scaled, index 1.4. Scales on the opercle were often embedded. No teratological development was observed.

ADDITIONAL CROSSES. Matings wre made between progeny of intersubspecific hybrids (reciprocal only), progeny of similar subspecies and progeny of intersubspecific hybrids, and wild stock of the following subspecies: *squamosum* × *squamosum*, *squamosum* × *spectabile*, *pulchellum* × *squamosum*, and *pulchellum* × *spectabile* from White River, Missouri.

No differences in coloration were detected between reciprocal crosses. The progency of each mating were essentially intermediate between the parental kinds. This, of course, in crosses between pure parental strains, could result from incomplete dominance in several or many factors; but such seems not to be the case here as shown by the fact that, in every instance, backcross progeny were rather uniformly intermediate (showing no evidence of Mendelian segregation) between the F_1 and the parental type to which they were backcrossed. Involvement of a large number of characters regulated by multiple factors is suggested as a genetic mechanism controlling these characters.

Data other than those on coloration are presented in Table 16 for all laboratory crosses.

DISCUSSION. Decrease in length of the cephalic (posterior infraorbital and supratemporal canals) portion of the acoustico-lateralis system occurred in almost all laboratory crosses. Branson and Moore (1962) review the literature on correlation of lateral-line morphology with species ecology. Active swimmers or bottom-dwelling species inhabiting swift currents possess a better developed acoustico-lateralis system than do sluggish swimmers or bottom-dwelling species inhabiting slow currents. There is no doubt that the laboratory environment was more lentic than that in which the orangethroat is normally found. Currents under laboratory conditions would be mainly vertical and produced by stand-tubes of the under-gravel filters. Whether these mild currents were responsible entirely for decrease in canal lengths (reduction of posterior infraorbital pores) is questionable. Collette (1962) relates decrease in the number of infraorbital pores and incompleteness of the supratemporal canal, in the darter *Etheostoma fusiforme* (Girard), to low productivity of the habitat in which these darters occur. In the original intrasubspecific breeding experiment (A × A, B × B; for identification of symbols, see legend of Table 16), the mean number of posterior infraorbital pores decreased progressively in the F_1 and F_2 progeny. F_1 progeny (AB, BA) of original intersubspecific crosses (A × B and B × A) and F_2 progeny (ABAB) also demonstrate a decrease in the mean number of pores, but in F_2 progeny (BABA) the mean number of pores again is that of the parental female (A). Results with backcrossing demonstrate that the mean number of infraorbital pores is greater than that of either parent population in the progeny of two crosses (AABA and BABB), is intermediate to those of the parent populations in the progeny of four crosses (AAAB, BAAB, ABBB, and BBBA; the mean number of pores of the latter is equal

to that of the parental male, BB), and is less than that of either parent generation in the progeny of two crosses (BBAB and ABBA). The progeny (BC) of another intersubspecific cross (B × C) demonstrates an increase over that of either parent in the mean number of pores, while the progeny (BD) of yet another cross (B × D) have a mean number of pores equal to that of the parental male.

If the development of posterior infraorbital pores was under direct influence of the environment, I would expect progressive decrease in number of pores with each succeeding laboratory cross, but because the mean number of pores increased or remained intermediate in the progeny of two F_1, one F_2, and most backcross generations, I suspect that this character like that of coloration is regulated by multiple genetic factors.

Factors influencing squamation of the cheek, opercle, nape, and breast seem to be chiefly hereditary. Progeny usually are intermediate in anterior scale index between the parental forms. In only one cross were the progeny (BB) less scaly than either parent. Scale exposure, however, seems to depend on the characteristics of the female parent. The progeny (AB) of male *spectabile* and female *pulchellum* have the opercle scales mostly embedded; in progeny of the reciprocal cross (BA) the opercle scales are well exposed.

Developmental malformations appeared rarely in the experimental crosses, but when they did they appeared in such numbers as to remove chance as a factor for their presence. The first malformations appeared during the second year of experimentation in the F_2 progeny BABA, backcross progeny BBAB, and F_1 progeny CA and BD. In the BABA progeny, 63 per cent of all the specimens reared had one or both pelvic fins malformed; all BBAB and BD progeny had one or both dorsal fins malformed; about one-half the CA progeny had the dorsal fins and/or the operculum malformed. Factors responsible for these teratologies only can be surmised because of the meager evidence at hand. Dietary deficiencies could lead to eggs of poor "quality," hence low survival and anomalous development. Even though all darters were fed the same diet in abundant quantities, it is conceivable that some tanks of darters may not have benefited from this diet, especially if a tank harbored a large population of hydra. Close watch was kept on the fry-tanks to keep this coelenterate in check, but less attention was paid to tanks containing juvenile and adult fishes, because hydra seemed to have no direct effect on larger fishes. Consequently, brood stock of some crosses may have not been as well fed as others.

The small number of anomalous F_1 progeny (CA and BD) suggests that more information is needed about the reciprocal crosses (AC and DB) before any conclusions can be drawn. About 24 DB progeny are being reared currently; these show no obvious fin abnormalities.

Differences do exist, however, among the gametes of geographic variants of *E. spectabile* which may account for some of the anomalies observed in

laboratory crosses. Hubbs and Strawn (1957a) report that eggs of *E. s. spectabile* from Arkansas (White River) are smaller, more delicate, and have a far lower survival rate than eggs of *E. s. pulchellum* from Texas. Additional matings are necessary to ascertain the effects gametic differences have on progeny of matings between geographic variants of *E. spectabile*.

SUMMARY AND CONCLUSIONS

Etheostoma spectabile is a darter inhabiting upland, hardwater streams of the Mississippi Valley and western Coastal Province.

Three subspecies are described as new and several proposed races and subraces are based on one or more of the following characters: coloration (primarily on color and pigmentation, especially of the male), squamation, development of the acoustico-lateralis system, and number of rays in the pectoral fin.

Etheostoma spectabile spectabile is the most variable member of the subspecies complex and, as here restricted, is composed of five races, several of which are comprised of subraces. The northern Ozark race includes orangethroats in tributaries of the Missouri River from its confluence with the Osage River eastward, in tributaries of the Mississippi River from southern Iowa south to its confluence with the Ohio River, and in tributaries of the upper Black and St. Francis rivers. The southern Ozark race includes orangethroats from White River of Missouri and Arkansas, from the headwaters to the confluence with Black River. The northeastern race includes populations from tributaries of western Lake Erie and the Ohio River, exclusive of the Tennessee, Cumberland, and Green rivers of Kentucky and Tennessee. The southeastern race includes orangethroats of the Tennessee, Cumberland, and Green rivers. *E. s. spectabile* intergrades with *E. s. pulchellum* in tributaries of the Missouri River west of its confluence with the Osage River to its confluence with the Kansas River and in some eastern tributaries of the Kansas River.

Etheostoma spectabile uniporum (a new subspecies) is separated from the range formerly attributed to *E. s. spectabile*. *E. s. uniporum* inhabits the western tributaries of Black River from Butler County, Missouri (Cane Creek) to Lawrence County, Arkansas (Flat Creek); the major tributaries occupied are Current, Eleven Point, and Spring rivers. *E. s. uniporum* resembles *E. s. spectabile* in coloration of the fins and is somewhat similar to *E. s. pulchellum* in coloration of the body. Scale characteristics, however, most closely resemble those of *E. s. spectabile*. In addition *E. s. uniporum* possesses a less well developed acoustico-lateralis sytem and a lower number of pectoral fin rays than other members of the subspecies complex. This subspecies probably differentiated from Ozarkian stock in the western tributaries of Black River where it now occurs.

Etheostoma spectabile fragi (a new subspecies) is separated from the range formerly assigned to *E. s. spectabile*. *E. s. fragi* inhabits the tributaries of Strawberry River, a western tributary of Black River immediately south of Spring River alluded to above. *E. s. fragi* is the most scaly-headed member of the subspecies complex and resembles *E. s. uniporum* most closely in coloration. *E. s. fragi* may have evolved from autochthonous stock in Strawberry River; alternatively it may have arisen by hybridization between "pro"-*uniporum* and a lowland scaly-cheeked darter (possibly *E. asprigene*).

Etheostoma spectabile pulchellum, as restricted herewith, ranges from the North Platte River of Nebraska to the Guadalupe River of Texas. It varies little in coloration throughout its range, the most variation being in the eastern portion of the Kansas River (intergrades with *E. s. spectabile*), eastern Arkansas River (red color prevalent), and some eastern tributaries of Red River (hybridizes with *E. radiosum*). *E. s. pulchellum* differs from other members of the subspecies complex in having the anterior region largely free of scales and distinctive coloration. This subspecies may have evolved from "pro"-*pulchellum* stock isolated in the northwestern tributaries of the Teays-Mississippi System (early Platte River or a more southern tributary) by Kansan glacial ice, and spread southward via the Ancestral Plains System after retreat of the glacier.

Etheostoma spectabile squamosum (a new subspecies) most closely resembles *E. s. pulchellum*, but differs from it by having a more scaly anterior region and distinctive coloration. *E. s. squamosum* inhabits streams draining the western slope of the Springfield Plateau and is separated from the range formerly attributed to *E. s. pulchellum*. This subspecies possibly evolved from a *pulchellum*-like ancestor in the tributaries where it now occurs, but in addition, by means of unidirectional hybridization, it may have incorporated some of the genome of related species (*E. caeruleum* or *E. whipplei*) with whom *E. s. squamosum* shares several characteristics.

Etheostoma spectabile probably evolved in the Ozark Highlands not later than late Pliocene or early Pleistocene, and dispersed via preglacial pathways into much of the Teays-Mississippi River System. Multiple glaciation must have forced the orangethroat southward and isolated populations in the Plains, Ozark Plateaus, and Interior Low Plateaus long enough for populations to differentiate but not long enough for these isolated populations to establish biological barriers. Interglacial periods allowed some populations previously isolated to make contact and intergrade. Drainage changes concomitant with Pleistocene climatic change also isolated some populations, while allowing others to expand their range and intergrade with populations from which they were isolated previously.

Natural hybrids occur between *E. spectabile* and other darters with similar mating habits when two species are either forced to spawn in the immediate area or when the number of individuals of one species greatly exceeds that

of the other at the spawning site; however, hybrid swarms occur rarely throughout the range of the species.

Breeding experiments between morphological variants of *E. spectabile* yielded progeny intermediate in most characters between the parental stock, with the exception of the degree of development of the acoustico-lateralis system. Anomalous progeny of some matings may indicate gametic differences between some populations or abnormal conditions under which matings were made or progeny were reared in the laboratory.

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Table 1. Comparison of the five subspecies of *Etheostoma spectabile*. Values given are means (to two decimal places) or modal numbers (integers).

Character	*spectabile*	*uniporum*	*fragi*	*pulchellum*	*squamosum*
Dorsal spines	9.92	10.12	10.29	9.79	9.73
Dorsal rays	12.69	12.14	12.30	12.77	13.05
Soft anal rays	6.97	6.71	6.63	6.73	6.60
Left pectoral rays	12.01	11.44	11.57	11.96	11.98
Lateral line scales	44.36	45.51	49.72	49.95	48.50
Pored scales	25.67	22.43	34.50	31.24	29.86
Diagonal scales	12	12	13	13	13
Scales above lat. line	5	5	6	6	6
Cheek scale index	1.08	1.21	2.91	0.74	2.04
Opercle scale index	2.24	1.72	2.90	0.27	1.96
Nape scale index	2.22	1.59	2.74	1.30	2.84
Breast scale index	0.37	0.17	1.39	0.00	1.03
Anterior scale index	1.48	1.17	2.48	0.58	1.97
Posterior infraorbital pores	2.94	1.45	2.88	2.82	3.42
Complete supratemporal canal	88%	32%	94%	85%	84%
Junction gill membrane index	1	1	2	2	2

TABLE 2. Frequency distribution of lateral line scales in populations of *Etheostoma spectabile spectabile* in several major rivers, and in intergrades[4] with *Etheostoma spectabile pulchellum*.

Drainage	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	n	$\bar{X}$
Tennessee	1	1	6	8	17	15	8	6	4	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	68	39.74
Cumberland (upper)	..	..	..	2	2	9	10	18	12	6	3	2	2	..	..	..	..	..	..	..	..	..	..	..	..	66	42.14
Cumberland(lower)	..	2	5	12	12	11	3	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	49	39.04
Green (upper)	..	..	..	..	..	..	..	..	..	1	3	3	4	1	2	1	1	1	..	..	..	..	..	..	..	17	47.29
Green (lower)	..	..	1	7	9	18	17	16	11	4	5	..	..	..	1	..	..	..	..	..	..	..	..	..	..	89	41.19
Ohio (S)[1]	..	..	..	..	..	..	5	4	13	9	28	20	15	15	10	4	1	1	..	..	..	..	..	..	..	125	45.81
Ohio (N)[2]	..	..	..	2	4	6	18	32	39	31	28	11	8	2	2	1	..	..	..	..	..	..	..	..	..	184	43.38
Missouri (E)[3]	..	..	..	..	..	..	3	3	6	12	25	18	26	28	34	20	14	7	8	5	1	..	..	..	..	210	47.84
Missouri (W)[4]	..	..	..	..	..	..	..	1	16	21	24	34	34	13	28	12	12	7	1	2	..	1	..	..	..	206	47.01
Mississippi[5]	..	..	..	..	2	14	10	12	19	15	24	18	13	4	9	4	..	..	..	1	..	..	..	..	..	145	44.38
Black-St. Francis[6]	..	..	..	1	..	..	1	4	..	5	7	6	6	1	5	..	1	1	..	..	..	..	..	..	..	38	45.68
White (upper)	..	..	..	..	..	..	..	..	..	..	1	1	1	2	5	11	11	16	15	9	10	..	4	1	1	88	52.25
White (lower)	..	1	1	5	5	15	16	18	22	22	18	21	9	8	3	3	2	1	..	..	..	..	..	..	..	170	43.64

[1] Southern tributaries east of Green River. [2] Northern tributaries and Lake Erie. [3] Osage River eastward. [4] West of Osage River (intergrades). [5] Tributaries from Iowa to Kentucky exclusive of Missouri and Ohio Rivers. [6] Upper Black River (Poplar Bluff, Mo. northward).

Table 3. Frequency distribution of lateral line scales in populations of *Etheostoma spectabile uniporum* in several stream systems, and in *Etheostoma spectabile fragi* (Strawberry River).

Drainage	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	n	$\bar{x}$
Cane Creek		..	..	..	..	1	1	1	4	6	2	3	1	1	..	..	..	20	48.10
Current River		2	4	8	6	5	9	10	6	7	5	4	..	1	..	..	..	67	45.34
Fourche River	.	1	3	3	1	4	7	3	5	1	1	2	..	..	..	..	..	31	44.94
Eleven Point River	1	..	4	3	9	11	6	5	5	1	..	2	..	..	..	..	..	47	44.32
Spring River		2	5	2	4	7	11	7	6	4	2	1	..	..	..	..	..	51	44.86
Strawberry River	..	..	..	..	3	..	5	4	6	12	19	16	17	15	5	4	3	109	49.72

Table 4. Frequency distribution of lateral line scales in populations of *Etheostoma spectabile pulchellum* in several major rivers, and in *Etheostoma spectabile squamosum* (Grand and Illinois rivers).

Drainage	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	n	$\bar{x}$
Kansas (upper)	..	1	2	8	8	18	24	39	29	28	30	16	7	2	3	1	..	..	..	..	..	..	216	47.85
Kansas (lower)	..	..	1	1	3	6	10	12	14	18	23	8	6	4	4	..	..	1	..	..	..	..	111	48.83
Arkansas (upper)	..	..	..	..	2	4	5	9	13	18	29	16	13	12	9	3	2	..	..	..	..	..	135	50.13
Grand River	1	..	5	3	11	18	19	22	32	21	28	10	4	1	2	1	..	..	..	..	..	..	178	47.64
Illinois River	..	..	1	3	..	5	12	23	40	53	48	30	22	6	7	3	1	..	..	..	..	..	254	49.36
Arkansas (lower)	..	..	..	..	2	10	14	23	23	23	46	32	31	26	8	6	6	1	..	1	..	1	253	50.16
Red (upper)	..	..	..	1	..	2	2	4	8	9	14	15	9	4	4	1	..	1	..	..	..	..	74	50.15
Red (lower)	..	..	1	3	1	2	3	7	6	4	8	3	..	..	1	..	..	..	..	..	..	..	39	47.77
Brazos	..	..	..	..	..	..	..	..	1	2	4	4	4	5	4	1	6	1	1	..	..	..	33	52.88
Colorado	..	..	..	..	..	2	1	3	6	10	4	2	5	4	1	..	..	..	..	..	..	..	38	49.55
Guadalupe	..	..	..	..	..	1	..	..	5	4	22	12	14	4	13	4	1	..	..	..	..	..	80	51.39

TABLE 5. Frequency distribution of pored scales in populations of *Etheostoma spectabile spectabile* in several major rivers, and in intergrades[4] with *Etheostoma spectabile pulchellum*.*

D	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	n	$\bar{X}$
T	1	..	1	2	..	3	4	4	10	7	17	8	2	6	2	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	68	21.18
Cu	..	..	..	..	1	..	..	..	..	2	1	6	5	5	8	8	7	5	5	8	3	1	..	..	..	..	1	..	..	..	..	66	27.17
Cl	..	..	1	..	..	2	4	8	8	8	6	6	2	2	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	49	20.84
Gu	..	..	..	..	..	..	..	..	1	2	2	..	..	4	2	2	2	..	2	..	..	..	..	..	..	..	..	..	..	..	..	17	25.18
Gl	..	..	..	..	..	..	..	3	4	4	3	13	5	11	18	10	12	2	2	2	..	..	..	..	..	..	..	..	..	..	..	89	25.11
OS	..	..	2	..	..	..	..	1	5	5	5	10	19	25	17	15	9	2	8	2	..	..	..	..	..	..	..	..	..	..	..	125	25.06
ON	..	..	..	..	..	..	..	..	3	4	3	7	13	29	19	26	20	18	17	11	3	4	2	3	..	2	..	..	..	..	..	184	27.24
ME	..	..	..	..	..	..	..	..	2	6	1	14	17	22	16	20	24	24	17	14	16	4	6	2	3	2	..	..	..	..	..	210	27.79
MW[4]	..	..	..	..	..	..	..	..	1	5	9	7	7	18	19	29	26	19	25	19	11	6	2	1	1	1	..	..	..	..	..	206	27.78
M	..	..	..	..	..	1	2	2	6	6	8	14	15	25	13	20	12	12	4	2	2	..	..	..	1	..	..	..	..	..	..	145	25.27
BSF	..	..	..	1	..	2	..	..	2	1	5	5	..	4	5	3	3	1	2	2	1	..	1	..	..	..	..	..	..	..	..	38	24.92
Wu	..	..	..	..	..	..	..	..	..	..	..	..	..	1	3	2	6	2	7	10	8	5	14	8	5	3	5	4	2	2	1	88	33.19
Wl	..	..	..	..	1	2	..	7	8	12	18	21	9	14	18	11	12	9	14	5	7	1	..	..	..	..	1	..	..	..	..	170	25.13

* For explanation of abbreviated drainage (stub) refer to Table 2 including footnote.

TABLE 6. Frequency distribution of pored scales in populations of *Etheostoma spectabile uniporum* in several stream systems, and in *Etheostoma spectabile fragi* (Strawberry River).

Drainage	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	n	$\bar{x}$
Cane Creek	..	..	..	..	..	..	..	2	1	1	1	3	1	3	1	2	2	..	2	1	..	..	..	20	22.80
Current River	1	..	1	1	2	2	5	5	5	9	7	10	9	2	3	1	1	3	..	..	..	..	..	67	19.66
Fourche River	..	..	..	..	..	..	1	..	..	3	..	4	2	4	1	7	1	2	1	2	2	1	..	31	24.16
Eleven Point River	..	..	1	..		..	2	2	7	4	..	11	2	6	6	6	..	..	..	..	..	..	..	47	21.00
Spring River	..	..	..	..	..	..	..	..	..	..	1	5	5	8	9	9	7	1	1	1	1	1	2	51	24.53

Drainage	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	n	$\pm$
Strawberry River	..	..	1	1	2	1	5	9	7	18	15	11	8	9	10	6	2	3	1	..	..	..	109	34.50

TABLE 7. Frequency distribution of pored scales in populations of *Etheostoma spectabile pulchellum* in several major rivers, and in *Etheostoma spectabile squamosum* (Grand and Illinois rivers).

Drainage	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	n	$\bar{x}$
Kansas (upper)	..	..	1	2	..	..	8	7	12	20	23	32	34	32	21	14	5	3	2	..	..	..	..	216	31.38
Kansas (lower)	..	..	2	3	4	6	10	13	11	11	6	22	8	5	2	2	4	..	1	..	1	..	1	111	30.19
Arkansas (upper)	..	..	..	..	..	2	2	7	3	15	11	20	14	17	12	11	9	5	4	2	..	..	1	135	32.17
Grand River	1	..	3	3	7	7	12	22	29	18	23	17	18	19	4	1	2	2	..	..	..	..	..	178	28.90
Illinois River	1	..	1	2	1	1	7	12	28	38	34	28	28	28	24	5	7	4	2	..	2	1	..	254	30.81
Arkansas (lower)	..	1	..	1	6	13	13	17	18	22	31	29	32	14	23	19	8	3	..	1	1	1	..	253	30.56
Red (upper)	..	..	..	..	..	3	..	1	5	3	10	15	9	10	6	3	4	2	3	..	..	..	..	74	31.80
Red (lower)	..	..	1	1	2	2	3	4	4	5	5	5	2	4	..	1	..	..	..	..	..	..	..	39	28.77
Brazos	..	..	..	..	..	..	1	1	..	1	1	3	4	3	3	4	4	2	2	1	2	1	..	33	34.18
Colorado	..	..	1	..	..	..	..	..	3	..	6	4	7	10	2	1	2	1	1	..	..	..	..	38	31.95
Guadalupe	..	..	1	1	1	4	6	4	6	8	7	10	15	8	4	..	3	2	..	..	..	..	..	80	30.19

TABLE 8. Frequency distribution of indices of anterior squamation in populations of *Etheostoma spectabile spectabile*, and in intergrades[4] with *Etheostoma spectabile pulchellum*.

	Cheek						Opercle					
Drainage*	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Tennessee	..	34	20	10	64	1.62	..	1	9	54	64	2.83
Cumberland (U)	..	66	5	..	71	1.07	1	28	21	21	71	1.87
Cumberland (L)	.	55	1	1	57	1.05	..	..	..	57	57	3.00
Green (U)	.	19	..	..	19	1.00	..	17	2	..	19	1.10
Green (L)	..	80	7	..	87	1.08	..	2	12	73	87	2.82
Ohio (S)[1]	1	121	2	..	124	1.01	11	65	24	24	124	1.49
Ohio (N)[2]	..	159	5	..	164	1.03	..	37	71	56	164	2.12
Missouri (E)[3]	..	186	18	..	204	1.09	..	8	26	170	204	2.79
Missouri (W)[4]	.. 25	146	..	..	171	0.85	7	86	49	29	171	1.58
Mississippi[5]	 1	155	2	..	158	1.01	..	10	41	107	158	2.61
Black-St. Francis[6]	..	35	3	..	38	1.08	..	7	13	18	38	2.29
White (U)	6	57	..	..	63	0.90	..	45	15	3	63	1.33
White (L)	..	128	2	..	130	1.02	..	14	25	91	130	2.59

	Nape						Breast					
Drainage*	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Tennessee	..	..	1	63	64	2.98	16	19	29	.	64	1.20
Cumberland (U)	..	22	24	25	71	2.04	46	24	1	..	71	0.37
Cumberland (L)		..	..	57	57	3.00	2	10	45		57	1.75
Green (U)	..	13	6	..	19	1.32	18	1	..	..	19	0.05
Green (L)	..	..	6	81	87	2.93	15	65	7	..	87	0.91
Ohio (S)[1]	1	83	33	7	124	1.37	124	..	..	..	124	0.00
Ohio (N)[2]	2	31	100	31	164	1.98	163	1	..	..	164	0.01
Missouri (E)[3]	..	12	52	140	204	2.63	201	3	..	..	204	0.01
Missouri (W)[4]	29	101	24	17	171	1.17	171	..	..	..	171	0.00
Mississippi[5]	..	7	55	96	158	2.56	158	..	..	..	158	0.00
Black-St. Francis[6]	..	9	11	18	38	2.24	36	1	1	..	38	0.08
White (U)	..	53	10	..	63	1.16	63	..	..	..	63	0.00
White (L)	1	14	35	80	130	2.49	124	6	..	..	130	0.05

* For explanation of drainage refer to Table 2 including footnote.

TABLE 9. Frequency distribution of indices of anterior squamation in populations of *Etheostoma spectabile uniporum*, and in the Strawberry River population of *Etheostoma spectabile fragi*.

	Cheek						Opercle					
Drainage	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Cane Creek	1	19	..	..	20	0.95	4	14	2		20	0.90
Current River	..	57	14	8	79	1.38	6	60	10	3	79	1.13
Fourche River	..	26	4	..	30	1.13	..	..	30	..	30	2.00
Eleven Point River	1	59	14	..	74	1.18	..	13	30	31	74	2.24
Spring River	..	31	20	..	51	1.39	..	9	16	26	51	2.33
Strawberry River	..	1	8	101	110	2.91	..	2	7	101	110	2.90

	Nape						Breast					
Drainage	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Cane Creek	3	14	3	..	20	1.00	18	2	..	..	20	0.10
Current River	4	46	18	11	79	1.46	62	14	3	..	79	0.25
Fourche River	3	3	5	19	30	2.33	27	3	..	..	30	0.10
Eleven Point River	3	29	34	8	74	1.64	62	11	1	..	74	0.18
Spring River	4	21	22	4	51	1.51	41	10	..	..	51	0.20
Strawberry River	..	3	22	85	110	2.74	19	42	36	13	110	1.39

TABLE 10. Frequency distribution of indices of anterior squamation in populations of *Etheostoma spectabile pulchellum*.

	Cheek						Opercle					
Drainage	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Kansas (U)	166	36	..	..	202	0.18	175	27	..	..	202	0.13
Kansas (L)	24	82	3	..	109	0.81	29	25	22	33	109	1.54
Arkansas (U)	50	89	..	..	139	0.64	137	2	..	..	139	0.01
Arkansas (L)	34	192	..	..	226	0.85	224	2	..	..	226	0.01
Red (U)	14	70	..	..	84	0.83	77	7	..	..	84	0.08
Red (L)	23	16	..	..	39	0.41	30	..	1	8	39	0.67
Brazos	..	33	..	..	33	1.00	33	..	..	..	33	0.00
Colorado	..	37	1	..	38	1.03	38	..	..	..	38	0.00
Guadalupe	10	70	..	..	80	0.88	80	..	..	..	80	0.00

	Nape						Breast					
Drainage	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Kansas (U)	31	83	84	4	202	1.30	202	..	..	..	202	0.00
Kansas (L)	2	30	45	32	109	1.98	107	2	..	..	109	0.02
Arkansas (U)	26	101	9	3	139	0.92	139	..	..	..	139	0.00
Arkansas (L)	13	184	29	..	226	1.07	226	..	..	..	226	0.00
Red (U)	2	72	10	..	84	1.10	84	..	..	..	84	0.00
Red (L)	2	11	18	8	39	1.82	39	..	..	..	39	0.00
Brazos	2	31	..	..	33	0.94	33	..	..	..	33	0.00
Colorado	5	25	4	4	38	1.18	38	..	..	..	38	0.00
Guadalupe	..	53	25	2	80	1.36	80	..	..	..	80	0.00

TABLE 11. Frequency distribution of indices of anterior squamation in major populations of *Etheostoma spectabile squamosum*.

	Cheek						Opercle					
Drainage	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Grand	1	43	67	78	189	2.17	13	52	45	79	189	2.00
Illinois	1	83	99	66	252	1.90	13	80	72	87	252	1.92

	Nape						Breast					
Drainage	0	1	2	3	n	$\bar{\times}$	0	1	2	3	n	$\bar{\times}$
Grand	1	..	30	158	189	2.82	28	83	59	19	189	1.36
Illinois	..	1	35	216	252	2.85	114	105	28	5	252	0.70

TABLE 12. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in populations of *Etheostoma spectabile spectabile* and intergrades with *Etheostoma spectabile pulchellum*.

	Posterior infraorbital pores								Supratemporal canal		
Drainage*	1	2	3	4	5	com.	n	$\bar{\times}$	com.	n	% com.
Tennessee	..	12	46	6	..	..	64	2.91	57	64	89
Cumberland	1	23	77	18	1	3	123	2.96	110	123	89
Green	..	5	54	17	1	10	87	3.18	81	87	93
Ohio (S)[1]	1	29	82	12	..	..	124	2.85	100	124	81
Ohio (N)[2]	..	22	107	22	2	1	154	3.03	131	154	85
Missouri (E)[3]	..	77	150	24	..	..	251	2.79	155	164	94
Missouri (W)[4]	..	3	137	31	..	..	171	3.16	144	171	84
Mississippi[5]	3	79	67	8	..	1	158	2.51	141	158	89
Black-St. Francis[6]	..	9	18	11	..	..	38	3.05	33	38	87
White	..	27	123	65	3	1	219	3.20	196	219	89

* For explanation of drainage refer to Table 2 including footnote.

TABLE 13. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in major populations of *Etheostoma spectabile uniporum* and in the Strawberry River population of *Etheostoma spectabile fragi*.

	Posterior infraorbital pores								Supratemporal canal		
Drainage	1	2	3	4	5	com.	n	$\bar{\times}$	com.	n	% com.
Cane Creek	52	3	..	..	..	..	55	1.05	4	20	20
Current River	74	5	..	..	..	..	79	1.06	9	79	11
Fourche River	..	30	..	..	..	..	30	2.00	19	30	63
Eleven Point River	58	16	..	..	..	..	74	1.22	4	74	5
Spring River	5	45	1	..	..	..	51	1.92	31	51	61
Strawberry River	..	21	74	7	1	7	110	2.88	104	110	94

TABLE 14. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in populations of *Etheostoma spectabile pulchellum*.

	Posterior infraorbital pores							Supratemporal canal		
Drainage	1	2	3	4	com.	n	$\bar{x}$	com.	n	% com.
Kansas (U)	..	64	126	19	2	211	2.78	125	211	59
Kansas (L)	1	25	60	23	..	109	2.96	84	109	77
Arkansas (U)	..	41	68	15	1	125	2.79	101	125	81
Arkansas (L)	5	124	78	17	2	226	2.48	216	226	96
Red (U)	2	11	51	19	1	84	3.05	74	84	88
Red (L)	2	17	16	4*	..	39	2.59	9	9	100
Brazos	..	11	18	3	..	32	2.75	25	32	78
Colorado	..	7	21	8	2	38	3.03	32	38	84
Guadalupe		18	46	16	..	80	2.98	79	80	99

* One specimen with five pores.

TABLE 15. Frequency distribution of posterior infraorbital pores and condition of supratemporal canal in populations of *Etheostoma spectabile squamosum*.

	Posterior infraorbital pores							Supratemporal canal		
Drainage	2	3	4	5	com.	n	$\bar{x}$	com.	n	% com.
Grand	12	97	66	10	4	189	3.40	146	189	77
Illinois	5	132	102	6	7	252	3.44	226	252	90

TABLE 16. Results of experimental crosses between subspecies of *Etheostoma spectabile* (IO=number of pores in the posterior segment of the infraorbital canal, the range followed by the mean; CST=percentage of specimens having a complete supratemporal canal; ASI=anterior scale index; N=number of specimens from which data were taken; T=teratologic development, number of specimens, op=operculum, df=dorsal fins, pvf=pelvic fins; A=*spectabile* from Osage River, Kansas; B=*pulchellum* from Kansas River, Kansas; C=*squamosum* from Spring River, Kansas; D=*spectabile* from James River, Missouri; AB=F_1 generation or progeny of *spectabile* ♂ × *pulchellum* ♀; ABAA=progeny of F_1 ♂, [*spectabile* ♂ × *pulchellum* ♀] × F_1 ♀, [*spectabile* ♂ × *spectabile* ♀]).

	A♂	A♀	AA	AAAA	B♂	B♀	BB	BBBB	A♂	B♀	AB	ABAB
IO	2-2:2.0	2-4:2.8	2-3:2.2	1-3:2.1	3-4:3.2	2-4:3.2	2-3:2.3	2-3:2.1	2-4:3.2	2-4:3.2	2-3:2.5	1-4:2.3
CST	100	40	25	12	80	55	33	0	50	55	50	17
ASI	1.5	1.9	1.9	1.7	0.8	0.8	0.4	0.7	1.7	0.8	1.2	1.4
N	2	11	24	16	5	10	10	17	4	9	20	30
T	..	..	..	..	..	..	..	..	..	..	..	..

	B♂	A♀	BA	BABA	AAAB	AABA	BBAB	BBBA	BABB	ABBB	BAAB	ABBA
IO	3-4:3.2	2-3:2.5	2-3:2.1	2-3:2.5	1-3:2.4	2-3:2.8	2-2:2.0	2-3:2.3	2-3:2.4	2-3:2.4	2-3:2.3	1-3:2.0
CST	80	32	4	38	5	0	0	0	25	15	0	25
ASI	0.8	1.7	1.2	1.3	1.5	1.6	0.9	0.8	1.0	1.0	1.0	0.9
N	5	19	34	49	20	13	5	20	24	26	6	20
T	..	..	..	31, pvf	..	..	5, df	..	..	..	..	..

	C♂	C♀	CC	C♂	A♀	CA	B♂	C♀	BC	B♂	D♀	BD
IO	4	3-4:3.7	3-4:3.3	4	2	2-3:2.9	3	3	3-4:3.5	3	2	3-3:3.0
CST	100	67	0	100	0	0	100	100	50	100	0	40
ASI	2.8	1.8	1.8	2.8	1.8	2.1	0.9	3.0	1.8	0.5	1.5	1.4
N	1	3	12	1	1	7	1	1	2	1	1	5
T	..	..	..	..	..	3df:2op	..	..	..	..	..	5 df

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Rate of Species Diversity Restoration Following Stress in Freshwater Protozoan Communities

JOHN CAIRNS, JR.
Department of Zoology, University of Kansas*

ABSTRACT

Fresh-water protozoan communities inhabiting plastic troughs through which unfiltered Douglas Lake (Michigan) water flowed were exposed to pH and temperature shocks. The time required for the community to achieve a species diversity (i.e., number of species) comparable to that existing before the shock as well as the control diversity was studied. Diversity was the only characteristic studied. Others, such as numbers of individuals and nutritive relationships, though important, were beyond the scope of this study. The two most important conclusions to be drawn from this preliminary study are (1) the magnitude or intensity of the shock seems to be more important in reducing protozoan species diversity than its duration and (2) restoration of protozoan species diversity may require only a few hours if the shock is mild, but as much as five or six days for severe shocks. The latter is probably true only of pH, temperature and other shocks where there is no toxicant residual left in either substrate or organisms.

INTRODUCTION

Aggregations or communities of aquatic organisms are subjected to almost continual stress due to environmental changes, some of which are "natural" and others of which are due to the wastes of our highly industrialized society. It is stresses of the latter sort that prompted this investigation. It is a generally accepted axiom in ecology that a gross environmental stress exerted upon a diverse biological community consisting of a large number of species results in a reduction in species diversity (i.e., number) or a simplification of the system. Two of the earlier papers noting this phenomenon for aquatic communities of streams in Pennsylvania are those of

* Address September 1968—Dept. of Biology, Virginia Polytechnic Institute, Blacksburg, Virginia 24061.

Patrick (1949) and Patrick *et al.* (1954). A more recent report of studies of shock effects on a variety of organisms other than protozoans has been prepared by Newcombe (1966). The purpose of this investigation was to determine the time required for protozoan species diversity to reach former levels following a gross and abrupt application of stress. This does not imply the reattainment of a "community" structure identical to that existing before the stress was applied since this would have meant assessment of the number of individuals in addition to the diversity of species. Since many freshwater protozoan species are fragile and difficult to preserve and since the techniques used to this end may also cause destruction or distortion of many individuals, reliable estimates of the density of the various species were beyond the scope of this investigation. The assumption was made that the qualitative aspects of recovery necessarily preceded the quantitative and might therefore be considered the basis though not the only component necessary for complete recovery. In addition I have an unpublished study which suggests that restoration of quantitative relationships requires considerably more time than the restoration of species diversity. The general idea of "shock magnitude" has been discussed for diatoms by Fjerdingstad (1950), Cholnoky (1960), and briefly by Reimer (1965).

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METHODS AND PROCEDURES

All experiments were carried out in a series of the simple plastic troughs and reservoir tanks illustrated in Figure 1. The water used in these experiments came from an intake pipe in Douglas Lake placed about one foot from the bottom, about 35 feet from shore at a depth of about 17 feet. This was pumped directly to a storage tank located in the Aquarium Building of the University of Michigan Biological Station, and from there by gravity feed to various outlets within the building. Since the storage tank held only about 200 gallons of water, and since this was used for a variety of purposes, it is unlikely that the average retention time was over 4 hours. Water from

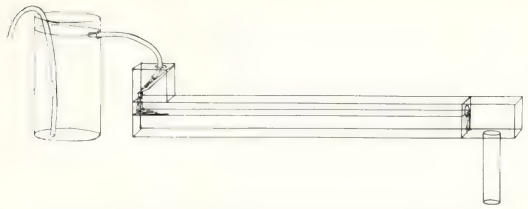


Fig. 1. Plastic reservoir and trough used in all experiments.

the outlets was taken through rubber tubing to one of the cylindrical plastic reservoirs (Fig. 1) and from there to the plastic trough paired with the reservoir. Each trough (Fig. 1) was 48 inches long, 2½ inches wide, and 3½ inches deep. A baffle was placed at the "upstream" end to insure that the entering water was thoroughly mixed and to reduce initial turbulence. A second baffle was placed near the outlet to produce a constant depth of 2 inches. Except for the height of the hole in the outlet baffle, the troughs used in these experiments are identical to those already described (Cairns and Yongue, 1968). The reservoir was added to the system to provide more uniform flow of the entering water and to achieve greater uniformity of flow. Average flow through each trough was approximately 100 ml per second, but with a crude system of this sort one may expect variations of = 20 percent. Similar or greater variations are not uncommon in natural streams. A 100 watt light bulb in a goose neck lamp was placed 18 inches above the mid-point of each trough and left on for 12 hours daily. The light intensity was not measurable with a Weston light meter during the remaining 12 hours.

The temperature and dissolved oxygen concentration of Douglas Lake water in South Fishtail Bay (where the intake pipe is located) for the summer of 1967 are given in Table 1. These and other characteristics for 1964 are given in Table 2. Several analyses (made with a Hach Model AL-36-WR kit, Hach Chemical Company, P.O. Box 907, Ames, Iowa 50010) of the reservoir water for dissolved oxygen concentration, carbon dioxide, pH and alkalinity indicated that the general characteristics were the same as those reported for 1964 although the dissolved oxygen concentration was usually over 5 ppm. However, the important consideration is that water of comparable quality was passing through all four systems at the same time except when altered for experimental purposes.

Several weeks were spent becoming familiar with the species inhabiting the troughs. Though some succession occurred, the appearance of new species was not sufficiently rapid to create identification problems. Samples were gathered from the bottom in the center of the tank by drawing a pipette from one side to the other at right angles to the direction of flow.

TABLE 1. Oxygen and temperature conditions in South Fishtail Bay, Douglas Lake, Cheboygan County, Michigan.

Date 1967 Conditions Depth (M)	June 30 Temp. °C.	O_2ppm	July 9 Temp. °C.	O_2ppm	July 11 Temp. °C.	O_2ppm
0	20.85	5.63	23.83	5.64	24.84	5.72
1	20.89	5.61	22.74	5.58	24.82	5.58
2	20.86	5.77	21.82	5.56	24.66	5.54
3	20.74	5.47	21.18	5.64	24.47	5.60
4	20.37	5.51	20.40	5.66	22.60	5.54
5	20.13	5.77	19.76	5.56	21.46	5.46
6	19.62	4.71	19.50	5.34	20.27	4.94
7	19.44	5.25	19.22	4.84	19.64	5.36
8	17.64	4.15	19.06	4.82	19.18	4.92
9	14.38	3.80	17.69	4.52	18.02	4.40
10	13.30	3.40	15.15	3.50	15.73	3.48
11	12.93	5.40	13.62	2.50	13.97	2.36
12	12.51	3.63	12.85	2.00	12.74	2.12
13	11.62	5.52	11.73	2.90	11.62	2.70
14	10.77	3.52	10.97	3.28	10.75	2.84
15	10.36	3.11	10.47	2.38	10.42	2.34
16	10.01	5.47	10.04	1.94	9.92	1.72
17	9.72	1.78	9.69	1.30	9.73	1.44
18	9.64	0.81	9.59	0.32	9.68	0.22
19	9.56	0.08	9.50	0.18	9.52	0.08
20	9.28	0.00	9.39	0.08	9.39	0.00
21	9.15	0.00	9.32	0.00	9.32	0.00
Bottom (21.5)			9.16		9.22	

Date 1967 Conditions Depth (M)	July 13 Temp. °C.	O_2ppm	July 15 Temp. °C.	O_2ppm	July 17 Temp. °C.	O_2ppm
0	20.76	5.10	21.45	5.16	20.04	5.10
1	20.78	5.10	21.34	5.28	20.05	5.14
2	20.78	5.00	21.20	5.20	20.00	5.14
3	20.72	5.04	19.88	5.20	10.81	5.28
4	20.71	5.08	19.64	5.24	19.55	5.24
5	20.65	5.12	19.55	5.20	19.28	5.02
6	20.63	5.18	19.43	5.08	19.13	4.88
7	20.59	5.04	19.35	5.02	18.97	4.78
8	20.19	5.16	19.29	4.96	18.73	4.70
9	19.43	5.46	19.01	4.92	18.62	4.52
10	18.14	4.02	18.57	4.54	18.15	4.10
11	14.20	3.66	17.18	4.32	17.67	3.90
12	12.68	2.12	13.86	2.52	14.90	2.52
13	11.81	2.56	11.95	2.44	12.76	2.08
14	11.09	2.68	11.00	2.20	11.02	2.16
15	10.26	2.00	10.61	1.48	10.70	1.70
16	9.98	1.24	10.10	0.84	10.12	1.20
17	9.84	0.56	9.85	0.26	9.84	0.10
18	9.70	0.10	9.71	0.14	9.61	0.04
19	9.55	0.06	9.58	0.04	9.48	0.00
20	9.49	0.04	9.50	0.00	9.42	0.00
21	9.41	0.00	9.30	0.00	9.20	0.00

Date 1967 Conditions Depth (M)	July 19 Temp. °C.	O_2ppm	July 21 Temp. °C.	O_2ppm	July 24 Temp. °C.[a]	O_2ppm
0	21.82	5.32	24.80	5.62	22.72	5.20
1	21.62	5.30	24.63	5.38	22.70	5.24
2	21.48	5.38	24.38	5.70	22.67	5.20
3	20.83	5.34	21.49	5.56	22.67	5.24
4	20.17	5.16	20.85	5.78	22.61	5.22
5	19.69	5.18	19.98	5.46	22.08	5.24
6	19.36	4.92	19.70	5.16	20.60	5.42
7	19.07	4.86	19.22	4.90	18.44	5.10
8	18.83	4.58	18.83	4.74	18.03	4.94
9	18.61	4.52	18.41	4.30	17.42	3.94
10	18.14	4.28	17.85	3.88	17.00	3.64
11	16.45	3.44	16.10	3.12	15.98	3.16
12	14.08	2.68	14.92	2.04	13.22	2.14
13	12.04	1.78	12.44	1.64	11.64	1.38
14	11.33	1.92	11.08	1.88	10.93	1.60
15	10.54	1.38	10.50	1.44	10.38	0.62
16	10.05	0.74	10.03	0.24	10.02	0.26
17	9.64	0.16	9.82	0.08	8.42	0.00
18	9.55	0.04	9.48	0.06	8.32	0.00
19	9.48	0.00	9.44	0.00	8.22	0.00
20	9.42	0.00	9.36	0.00	8.10	0.00
21	9.35	0.00	9.08	0.00	8.06	0.00

Date 1967 Conditions Depth (M)	July 26 Temp. °C.	O_2ppm	July 28 Temp. °C.	O_2ppm	July 30 Temp. °C.	O_2ppm
0	23.79	5.34	24.16	5.32	24.64	5.30
1	23.82	5.22	24.18	5.24	24.69	5.24
2	23.53	5.40	24.16	5.28	24.66	5.02
3	22.82	5.22	23.64	5.20	23.36	5.28
4	22.59	5.30	23.18	5.26	23.08	5.42
5	22.39	5.20	22.47	5.22	22.78	5.12
6	21.76	5.10	21.90	4.84	22.30	5.04
7	21.03	4.74	21.51	4.64	21.64	4.78
8	19.83	4.68	19.85	4.48	20.18	4.42
9	18.74	4.42	18.34	3.74	18.57	3.78
10	17.62	3.56	17.42	2.90	17.28	2.90
11	16.24	2.62	16.17	1.18	16.15	2.36
12	14.62	1.68	14.79	1.14	14.79	1.30
13	12.35	1.36	12.94	1.22	12.76	1.04
14	11.42	1.24	11.54	1.04	11.32	1.16
15	10.83	0.48	10.69	0.44	10.66	0.28
16	10.38	0.08	10.02	0.12	10.30	0.08
17	10.04	0.00	9.82	0.00	9.86	0.00
18	9.50	0.00	9.70	0.00	9.69	0.00
19	9.39	0.00	9.55	0.00	9.58	0.00
20	9.33	0.00	9.50	0.00	9.47	0.00
21	9.28	0.00	9.38	0.00	9.37	0.00

TABLE 1. Oxygen and temperature conditions in South Fishtail Bay, Douglas Lake, Cheboygan County, Michigan (Concluded).

Date 1967 Conditions Depth (M)	August 3 Temp. °C.	0_2ppm	August 6 Temp. °C.	0_2ppm
0	23.17	5.22	22.60	5.20
1	23.18	5.20	22.62	5.24
2	23.19	5.22	22.60	5.30
3	23.18	5.16	22.09	5.18
4	23.20	5.14	21.90	5.28
5	22.82	5.14	21.75	5.16
6	21.75	4.94	21.50	5.10
7	21.25	4.40	21.12	4.54
8	19.72	4.24	20.79	4.36
9	18.42	3.50	20.45	3.60
10	17.00	1.90	18.54	2.54
11	16.04	1.44	16.70	1.64
12	16.00	0.84	14.80	0.90
13	12.68	1.04	13.10	0.62
14	11.36	1.16	11.09	0.24
15	10.88	0.20	10.48	0.08
16	10.32	0.12	10.12	0.08
17	10.00	0.08	9.82	0.00
18	9.74	0.00	9.66	0.00
19	9.62	0.00	9.58	0.00
20	9.50	0.00	9.44	0.00
21	9.38	0.00	9.31	0.00

[a] Error possible in this temperature data because resistance thermometer did not properly align due to low batteries.

TABLE 2. Chemical and physical characteristics of Douglas Lake water, June 26, 1964.

Depth in Meters	Temp. °C.	pH	D.O.* in p.p.m.	Conductivity**	Free*** CO_2 in p.p.m.	Bicarbonate carbon in p.p.m.	Total Alkalinity in p.p.m.
0.0	19.80	8.42	10.43	252	1.08	30.01	126.2
1.0	19.78						
2.0	19.75						
3.0	19.73						
5.0	19.64						
6.0	18.99						
7.0	18.93	8.44	8.16	244	0.036	31.35	130.6
10.0	18.77						
12.0	17.64	8.12	7.37	258	12.4	30.06	127.6
14.0	13.33	8.01	6.64	262	2.57	29.80	
16.0	8.49	7.59	2.60	278	8.57	30.02	126.4
18.0	6.00	7.61	2.14	276	7.33	29.90	124.6
19.0	5.77	7.55	0.40	278	8.40	29.44	123.0
19.5	Bottom						

* Dissolved oxygen concentration.
** In micromhos corrected to 25° C.
*** Calculated.
Light Extinction Coefficients: Secchi disc 0.44
Photo-meter 0.58

This included in one sample the ten sampling points (as well as all intermediate points) which collectively produced a good estimate of total species diversity (Cairns and Yongue, 1968). Results obtained by Needham and Usinger (1956) with aquatic insects suggest that qualitative sampling of this type is quite reliable. Four samples were removed from this primary sample for microscopic examination. Identification to species was made whenever possible and those few species that were difficult to identify were examined in sufficient detail to insure their separation from other species present. The usual taxonomic keys were used for identification. Stains and other aids to identification were not used since densities were often low and the loss or distortion of fragile specimens would probably have skewed the results more than an occasional lumping of several species. Furthermore, the use of phase microscopy reduces the need for many conventional stains.

Two types of environmental stress were applied to these systems—pH and temperature changes. These had the advantage of being easily monitored without the analytical complications of heavy metals or complex organic compounds. In addition, the possibility of residual toxicants being left in the test troughs was eliminated. No attempt was made to duplicate "natural" conditions. However, anyone familiar with pollution in this country will realize that conditions approaching those in these experiments are not impossible in the waters of our industrial society. The pH was changed by temporarily shutting off the flow to the reservoir tank, adding either HCl or NaOH to the reservoir to produce the desired pH, and restoring flow to the system. Since water entered the bottom of the reservoir tank (Fig. 1) and left the top, this usually resulted in a strong initial shock in the trough followed by a gradual restoration of normal conditions. Temperature shocks were produced by placing lake water heated to appropriate temperatures in the reservoir tanks. As was the case for pH, an abrupt initial change was followed by a gradual return to normal. Readings were taken as rapidly as possible (at least four per minute) immediately above the substrate where the protozoans were sampled. The pH was determined with either paper or a Hach pH kit. Temperature was determined with a standard thermometer accurate to 0.1° C.

A possible source of error was that some of the very low density species recorded may have been merely individuals washed into the sample area and not really established there. To estimate the "wash-in" rate needed to introduce consistent errors of this type, substantial quantities of several cultured species were poured into the trough inlet water. These were extremely crude experiments, but they do provide some means of assessing the importance of this source of error. The cultures of *Paramecium bursaria* and *Peranema trichophorum* had an approximate density of 10 organisms per drop. These estimates were based on ten samples removed from various parts of the culture flask. Culture fluid (123 ml for each culture) containing

these species was introduced over a period of one hour by dropping it on the "upstream" baffle of the trough with the inflowing lake water. The *Euglena splendens* inoculum was prepared by centrifuging the culture to obtain an estimated density of 1000 individuals per drop and introducing the entire 63 cc at once by pouring it into the "upstream" end of the trough with the inflowing lake water. Sampling began immediately and was comparable to the sampling and counting procedures already described. These three species were selected because they were strikingly different from other species in the trough communities into which they were introduced and were thus easily identified. Control trough samples showed none of the three species.

RESULTS

The pH and temperature changes are illustrated in Figures 2, 4, 6, 8, and 10; and results of these experiments are shown in Figures 3, 5, 7, 9, and 11. Results for the inoculation with cultures of *Paramecium bursaria, Peranema trichophorum,* and *Euglena splendens* are given in Figures 12, 13, and 14.

In general the recovery rate was comparatively rapid. For example, a shock to 50° C. caused a drop from 26 to 7 species (Figure 3). Recovery to 18 species was achieved in 24 hours although recovery to original diversity didn't occur until between 72 and 144 hours. In contrast, the thermal shock to 40° C. (Figure 4) caused a comparatively slight reduction from 31 to 22 species with recovery to approximately control diversity in 72 hours (Figure 5). The relatively long but comparatively mild thermal shock of slightly over 30° C. for about 24 hours (Figure 6) reduced the diversity from 34 to 21 species in the first four hours (Figure 7) and then while the thermal shock was still in progress there was an increase of three species at 12 hours. A variation this small could easily have been due to sampling error, but it is interesting to note that the main reduction in species occurred in the first few hours of exposure and there was no significant reduction in diversity after that. However, the rapid restoration of initial species diversity after return to normal temperatures suggests that some temperature tolerant species began to invade the sampling site while the shock was in progress. The increase in species diversity at 12 hours would then be a preliminary indication of a trend rather than a sampling error.

A pH shock from about 7 to 14 (Figure 8) caused a reduction of species from 26 to 5 with recovery to 20 species at about 90 hours (the control had 26 species at that time) and finally to the same diversity as the control at 192 hours (Figure 9). Note that both control and test trough had a marked increase in species diversity between 90 and 192 hours though the control diversity had been quite stable before that. A pH shock from about 7 to 3 (Figure 10) caused a reduction from 34 to 18 species (Figure 11). Note that the shock was applied just before the end of the first 24 hour period (Figure 11).

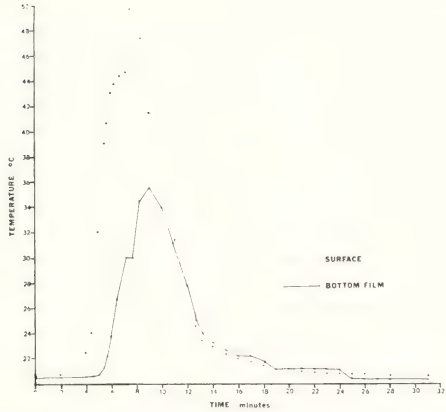


FIG. 2. Experiment 1—pattern of thermal shock from about 20° to 50° C. Note that the water flowing over the surface film has a much higher temperature than the bottom film which contains most of the protozoan species.

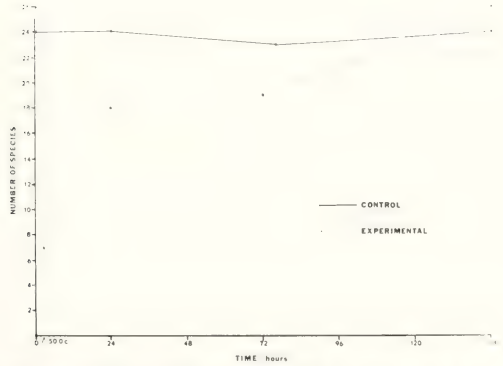


FIG. 3. Experiment 1—changes in species diversity following a thermal shock from 20° to 50° C.

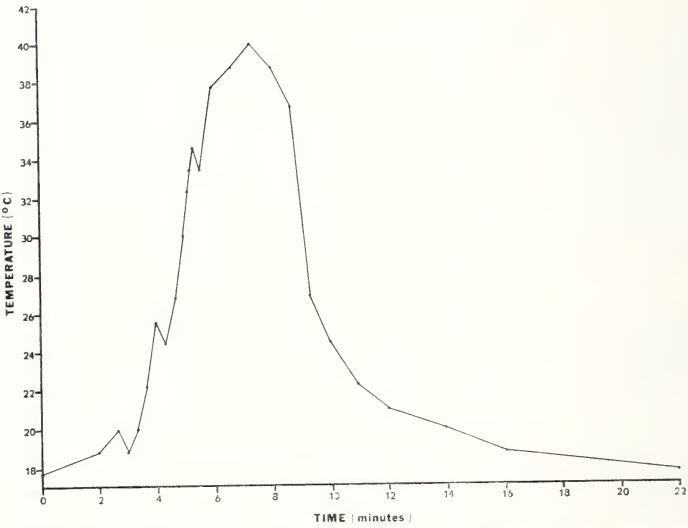


FIG. 4. Experiment 2—pattern of thermal shock from 18° to 40° C. and recovery to original temperature.

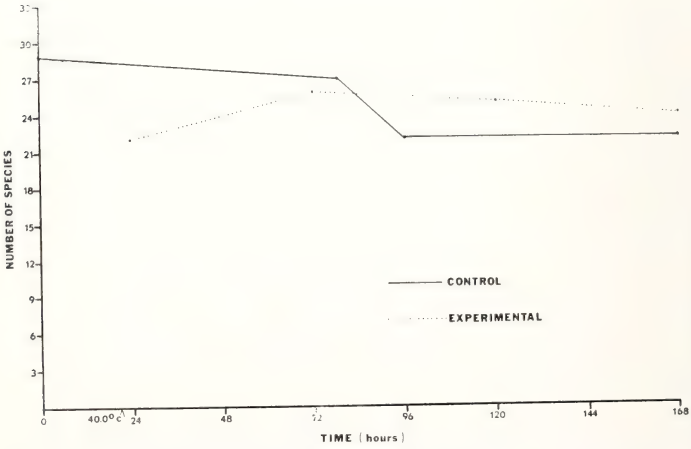


FIG. 5. Experiment 2—changes in species diversity (i.e., numbers of species) following a thermal shock from 18° to 40° C.

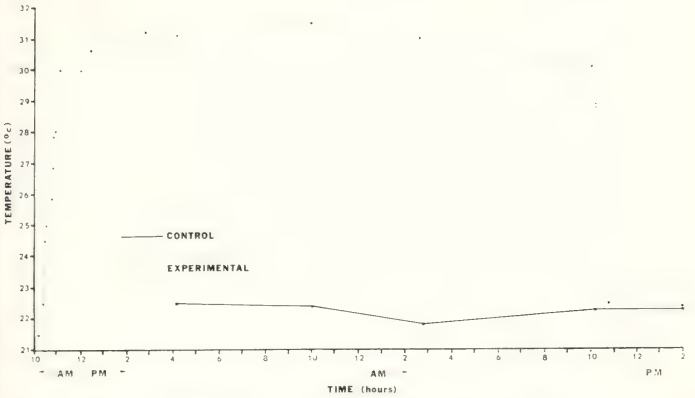


FIG. 6. Experiment 3—pattern of temperatures during 24 hour exposure to a high of 30-31° C.

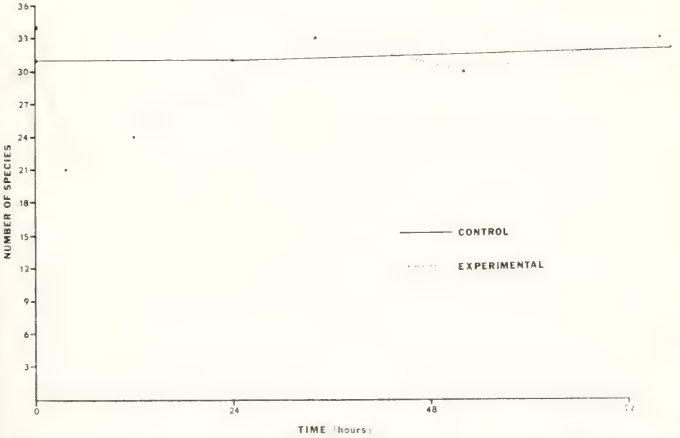


FIG. 7. Experiment 3—changes in species diversity following exposure to temperatures of 30-31° C. for approximately 24 hours.

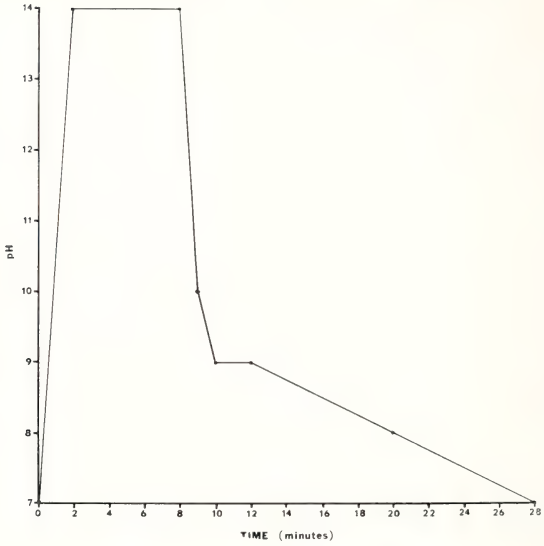


FIG. 8. Experiment 4—pattern of shock from pH7 to pH14.

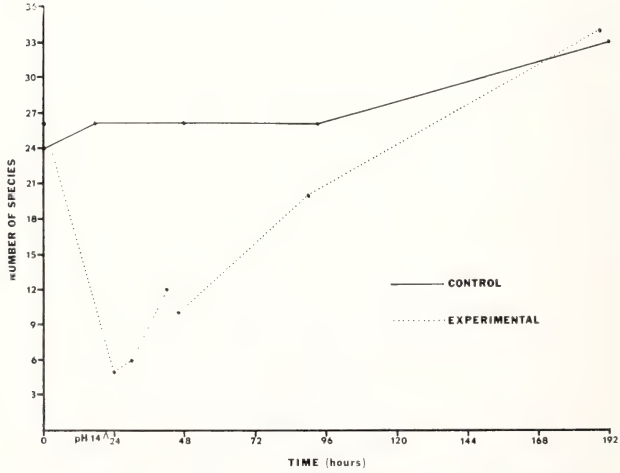


FIG. 9. Experiment 4—changes in species diversity (number of species) following a pH shock from 7 to 14.

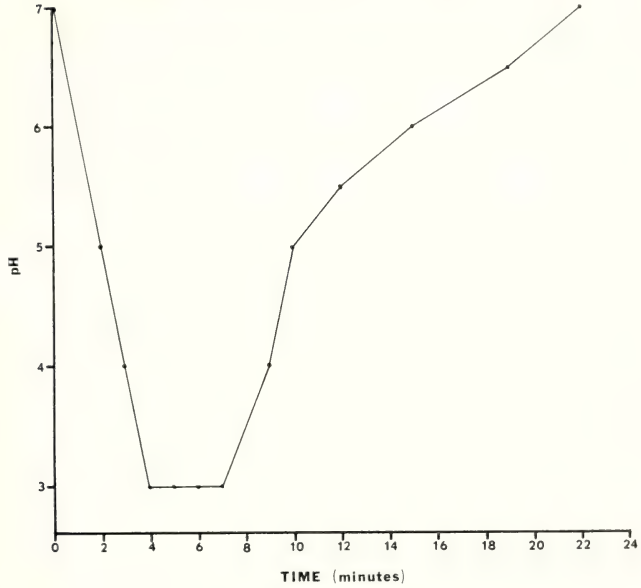


FIG. 10. Experiment 5—pattern of shock from pH7 to pH13.

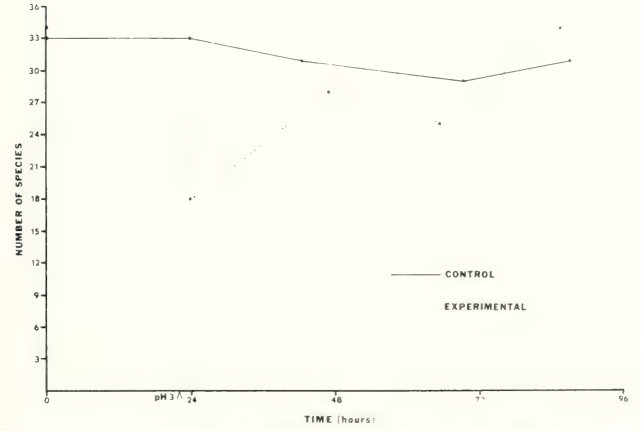
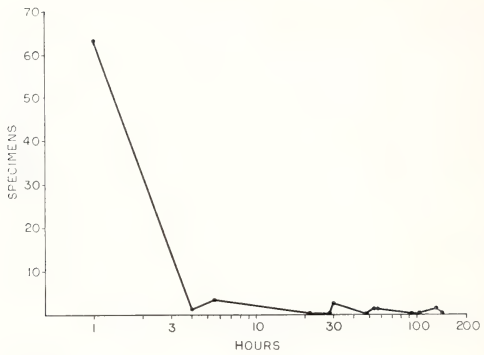


FIG. 11. Experiment 5—changes in species diversity following a shock from pH7 to pH13.


70
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SPECIMENS
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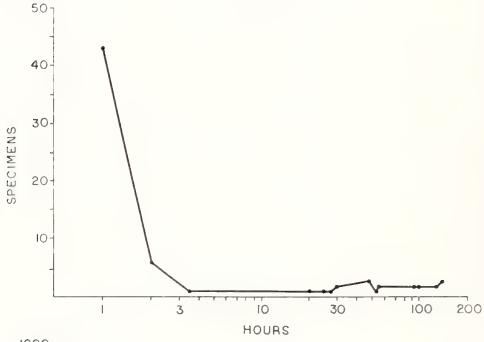
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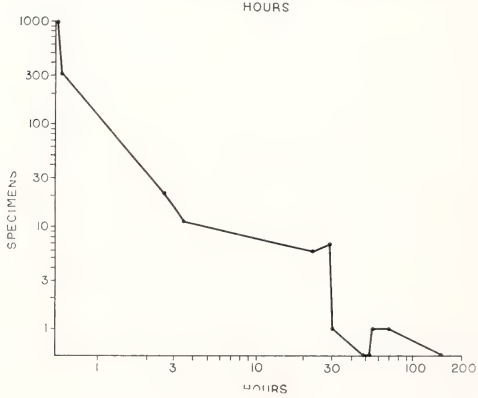
1000
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10
3
1
SPECIMENS
1
3
10
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HOURS

The numbers of *Paramecium bursaria, Peranema trichophorum* and *Euglena splendens* noted at the sampling site following massive introduction of individuals from cultures are shown in Figures 12, 13, and 14. Some dead or dying *Euglena splendens* were noted for three days although all specimens of the other two species appeared healthy and normal. The dying *Euglena* were not included in the record. It is quite obvious that the majority of individuals of all three species introduced were washed right through the system. One would assume that the environment was distinctly unfavorable to dying individuals of *Euglena splendens* though it was apparently at least marginally suitable for the few individuals that seemed to be in good condition. At any rate these results suggest that random washing in of a few odd specimens of various species would not have produced gross error.

DISCUSSION

The surface and subsurface waters in the troughs were quite well mixed by the inlet baffle. However, the bottom film in which the substrate associated protozoans lived did not receive the full impact of the shocks (Figure 2). Even with information on the general effect in the bottom film it would not be safe to assume that each protozoan was exposed to the full environmental shock. Therefore the shocks should only be regarded as changes in the water flowing through the troughs and not in the substrate films inhabited by protozoans. Though it would be interesting to know the precise conditions which "eliminated" (i.e., not observed in sampling) protozoans, the main goal of these experiments was to study the species diversity restoration following stress and not the exact stress needed to produce the observed reduction in diversity.

Most of the "replacement" species were the same as those "eliminated" (i.e., not observed in sampling) by the shock. This suggests that the invasion of species was qualitatively similar for several days at a time. Of course, new species were always appearing and others disappearing in both control and experimental troughs, but this gradual succession is characteristic of most microbial communities.

Though the number of species varied from the mid twenties to the low thirties before stress was applied, controls and experimental troughs usually had similar diversities for a given experiment. Oscillation is a characteristic of most biological systems and this probably applies to species diversity as well.

Fig. 12. Numbers of *Paramecium bursaria* noted at the sampling site following massive introduction at 0 hours at the trough intake.

Fig. 13. Numbers of *Peranema trichophorum* noted at the sampling site following massive introduction at 0 hours at the trough intake.

Fig. 14. Numbers of *Euglena splendens* noted at the sampling site following massive introduction at 0 hours at the trough intake.

Since data of this type are often used by non-biologists in water management and related fields, a word of caution may be advisable. First, these systems were not "natural" and assessment was made *only* of changes in species diversity. Many other parameters are needed to characterize an aquatic community. Second, this system (i.e., Douglas Lake Water, etc.) may have many unique characteristics and these results should not be used for water management until comparable experiments have been carried out in other situations. Finally, an aquatic community and ecosystem are complex affairs with an almost infinite number of interrelationships. It is important to realize that disturbance of one segment may send shock waves through the entire system, the impact of which may continue long after the site or biological group originally affected has returned to an approximation of its original state. The studies reported in this paper represent only the effect of two types of abrupt environmental changes upon a single characteristic of a protozoan community, species diversity.

CONCLUSIONS

The two most important conclusions to be drawn from this preliminary study are (1) the magnitude or intensity of the shock seems to be more important in reducing protozoan species diversity than its duration and (2) restoration of protozoan species diversity may require only a few hours if the shock is mild, but as much as five or six days for severe shocks. The latter is probably true only when there is no test material or toxicant residual left in either substrate or organisms as would have been the case had tetraethyl lead been used.

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Monograph of the Plant Genus *Porophyllum* (Compositae: Helenieae)[1]

R. ROY JOHNSON[2]

INTRODUCTION

The genus *Porophyllum* (COMPOSITAE-Helenieae) is native to the Western Hemisphere, occurring in southern Nevada, California, southwestern Texas, and Arizona south to southern Peru, northern Argentina, and southern Brazil. The first named species of *Porophyllum* were placed in *Cacalia* and *Kleinia*. The name *Porophyllum* was first validly published by Guettard in 1754[3] (see Generic Diagnosis), not by Adanson (1763) as has been previously thought true. Since neither Guettard nor Adanson used specific names, the first application of the generic name *Porophyllum* to a given species was applied in 1826 by Cassini (see synonomy under *Porophyllum ruderale* ssp. *ruderale*) in conjunction with the oldest available specific epithet (from *Kleinia ruderalis*).

Although DeCandolle (1836) listed all of the then known species of *Porophyllum*, and Rydberg (1916) treated the North American species, this study is the first complete monographic treatment of the entire genus. The genus may be divided into two sections, *Porophyllum* and *Hunteria*. Section *Porophyllum* occurs in the drier regions of South America as well as the more mesic areas of South, Central, and North America, and the West Indies. Section *Hunteria* is found in the arid and semi-arid parts of central and northern Mexico, and the southwestern United States. The species vary in distribution from those found practically throughout the entire range of the genus, such as *P. ruderale*, to those known only from a single collection, as *P. quinqueflorum* and *P. brachypodum*.

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[1] Based on a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Kansas, Lawrence, Aug., 1964.

[2] Center for Anthropological Studies, Prescott College, Prescott, Arizona.

[3] Thanks are due especially J. E. Dandy and also R. Ross, British Museum, for supplying this information.

The word *Porophyllum* is derived from the Creek *porus,* meaning pore or passage, and *phyllon,* leaf (Jaeger, 1955). The Greek spelling, *Porophyllon,* has occasionally been used for the genus (*fide* Rydberg, 1916). Because of the leaf glands of most species, the genus is commonly known as "pore-leaf" to English-speaking people. The inhabitants of the southwestern United States and Mexico call species in these regions "hierba del venado" (Martinez, 1937) or "yerba del venado" (Santamaria, 1942), meaning deer weed. Wildlife and cattle browse several species of *Porophyllum* (Kearney and Peebles, 1951). Overgrazing in southwestern Texas has played a major role in reduction of the range and numbers of *P. greggii* to the point of its near extinction and perhaps that of other species as well (see discussion under *P. greggii* and *P. gracile*).

Porophyllum ruderale subsp. *macrocephalum,* and probably *P. tagetoides,* is sold as a green vegetable in markets in Veracruz. The young shoots of *P. nutans* and *P. viridiflorum* are eaten raw in the state of Mexico. The natives of several countries often use certain species for medicinal purposes. The aromatic oils, contained largely in the pores or glands which are especially plentiful on the leaves, produce a strong odor when the foliage is bruised, broken, or heated. Cures, real or fancied, attributed to species of *Porophyllum* are probably largely due to either the soothing properties of the oils or the imagination by the patient that anything that is so odoriferous must be beneficial.

Leaves, stems, or roots are generally heated in water to make a strong tea which is taken internally or applied externally. The Moapa Piutes of Nevada use a root decoction and occasionally stems and leaves of *P. gracile* as a regulator for delayed menstruation (Train, *et al.,* 1957). *Porophyllum gracile* is also used by the natives of Baja California for intestinal disorders (Jaeger, 1940). An infusion from *P. punctatum* is employed as a remedy for gonorrhea in Yucatan (Standley, 1930). The Mexicans of Guaymas have used *P. pausodynum* to alleviate headaches (Robinson & Greenman, 1896). In Venezuela the roots of *P. ruderale* are used in treating snakebite and to relieve pain from rheumatism and erysipelas, a bacterial disease (Pittier, 1926).

ACKNOWLEDGEMENTS

The writer expresses appreciation to Dr. R. C. Jackson for originally suggesting this problem and for direction throughout much of its course. Part of this study was conducted during my term as a research assistant under Dr. Jackson's NSF Grant-G20864. Thanks are due also to Sigma Xi and Sigma Xi-RESA for a grant to travel throughout the southwestern United States and into Mexico, permitting field work as well as collection of materials for experimental studies, and to the University Research Institute of The University of Texas at El Paso for grant No. 2763. I am also grateful to the curators of the following institutions for allowing me to study materials in their care: University of Arizona (ARIZ), Arizona State University (ASU), Chicago Natural History Museum (F), Gray Herbarium of Harvard University (GH), University of Kansas (KANU), Lundell Herbarium of the Texas Research Foundation (LL), University of Michigan (MICH), Missouri Botanical Garden (MO), Notre Dame (ND), and Greene Her-

barium (ND-G), New Mexico State University (NMC), New York Botanical Garden (NY), Bebb Herbarium of the University of Oklahoma (OKL), Botanical Department of the Naturhistoriska Museum, Stockholm, Sweden (S), San Diego Natural History Museum (SD), Southern Methodist University (SMU), Sul Ross State College (SRSC), University of Texas at Austin (TEX), University of California at Berkeley (UC), University of New Mexico (UNM), U.S. National Herbarium (US), and Jardín Botánico, Madrid, Spain.

METHODS AND MATERIALS

This study entailed the examination of more than 3000 specimens from 22 herbaria, extensive field studies in the southwestern United States and Mexico, and studies of hybridization with *P. gracile*, *P. scoparium*, *P. amplexicaule*, and *P.* X *fruticulosum* (a natural hybrid between *P. amplexicaule* X *P. scoparium*). In addition *P. ruderale* subsp. *macrocephalum* was collected in various parts of Mexico and also grown in the greenhouse. Plants of *P. tridentatum* var. *crassifolium* and *P. punctatum* were also grown in the greenhouse.

Chromosome numbers are listed in Table 1. Clumping of meiotic metaphase chromosomes made counts difficult for most species; in addition, the chromosomes are small. The longest chromosome in any species examined was 2-3 μ. This was in a root tip of *P. ruderale* subsp. *macrocephalum* after treatment for 2 hours with 8-hydroxyquinoline.

Types were examined when possible, but in some cases either a photograph or drawing of the type was used. The protologues of names in synonomy were obtained and compared with type materials.

TABLE 1. Chromosome Numbers in *Porophyllum*.

Species	*n*	Plant Source
P. amplexicaule	12	COAHUILA, Saltillo (Turner, Beaman & Rock, 1961)
P. coloratum	12	MEXICO (R. C. Jackson, KU)
P. gracile	24	ARIZONA, Pima Co., Tucson Mts., RRJ 1777
P. punctatum	12	NUEVO LEON (Turner & Flyr, 1966)
P. ruderale subsp. *ruderale*?	11*	PERU, Cordillera Occidental (Diers, 1961)
	22*	PERU, Huanuco; COLUMBIA, Santander; COLUMBIA, Valle (Raven & Kyhos, 1961)
P. ruderale subsp. *macrocephalum*	11*	ARIZONA, Santa Cruz Co., Sycamore Canyon, Mason 2144 (Figs. 1, 2)
	11*	SINALOA (Turner & Flyr, 1966)
P. scoparium	12	TEXAS, El Paso Co., El Paso, RRJ 1547
P. tagetoides	12	OAXACO, 7 mi. e of Tierra Blanca (Powell & Turner, 1963)
P. tridentatum var. *crassifolium*	15	BAJA CALIFORNIA, San Bruno Island, Carter and Reese 4538 (Johnson, 1965)
P. viridiflorum	12	SAN LUIS POTOSI, 15 mi. e of Ciudad del Maiz (Powell & Turner, 1963)

*Haploid number obtained from somatic count.

Measurements were made with vernier calipers or a millimeter rule. Flowering time was obtained from dates on herbarium sheets, field notes, and the literature.

Localities for representative specimens were plotted on the appropriate map to show the distribution of each species. If any information is lacking for specimens cited, such as day of the month or collector's number, it was not available. Abbreviations for herbaria from which sheets were examined are according to Lanjouw and Stafleu (1964). Abbreviations for names of persons who have named taxa follow Fernald (1950). Species relationships and peculiarities, methods of differentiating between related species, and other pertinent information are given in the discussion following the distribution. Citation of specimens conforms to the method used in volume 16 of *Brittonia*.

GENERIC RELATIONSHIPS AND ORIGIN

Porophyllum has been placed traditionally in the tribe Helenieae, subtribe Tagetininae (Bentham, 1873; Hoffman, 1894). Bentham and Hooker (1873) and Gray (1886) placed the genus in the tribe Helenioideae. Rydberg (1915) placed *Porophyllum* in the tribe Tageteae, subtribe Tagetanae, or Tagetinae of Cassini (1829). Cronquist (1955) included this genus, as well as the other Helenieae, in the Heliantheae, stating that the single main criterion used for separation of the Helenieae from the Heliantheae (naked receptacle versus the chaffy receptacle of Heliantheae) is insufficient. In addition, certain genera (*fide* Cronquist, 1955) are intermediate in this character.

Despite differences of opinion regarding tribal or subtribal designation, it is generally agreed that *Porophyllum* is a member of a natural group composed of the genera *Adenopappus* Benth., *Chrysactinia* Gray, *Dyssodia* Cav., *Lescaillea* Griseb., *Leucactinia* Gray, *Nicolletia* Gray, *Pectis* L., and *Tagetes* L. (Johnston & Turner, 1962). All nine genera are characterized by the possession of glands bearing aromatic oils. Five genera have a pappus partially or entirely of squamellae. The other four have a pappus of bristles; in addition, *Chrysactinia* and *Leucactinia* have radiate heads, and *Porophyllum* and *Lescaillea* have discoid heads. *Lescaillea* has scalelike leaves in contrast to the well-developed leaves of *Porophyllum*. The heads of *Lescaillea* are much smaller than those of any species of *Porophyllum*, and the phyllaries each bear a single dorsal gland in contrast to several glands on the phyllaries of all species of *Porophyllum*. Thus, *Porophyllum* is the only genus of this group with the combination of discoid heads, pappus of bristles only, and well-developed leaves.

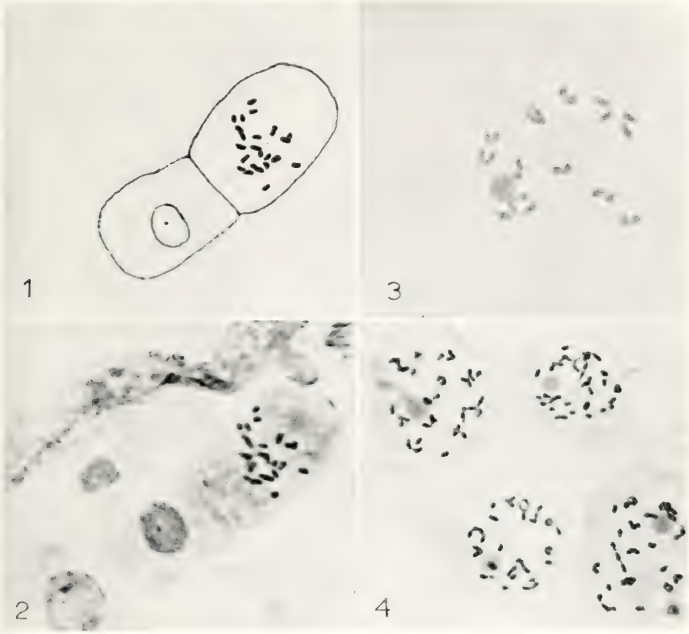

FIG. 1. Drawing of mitotic chromosomes in a root tip cell (Fig. 2) of *P. ruderale* subsp. *macrocephalum*—$2n=22$ (× 4650).

FIG. 2. Photograph of mitotic chromosomes in a root tip of *P. ruderale* subsp. *macrocephalum* (× 4650).

FIG. 3. Diakinesis, showing 12 bivalents, in a microsporocyte from *P. scoparium* (× 5335).

FIG. 4. Diakinesis in microsporocytes from *P. amplexicaule* (collected in the region of hybridization with *P. scoparium*) showing univalents, bivalents and multivalents (× 3880).

Small (1919) postulated that although *Porophyllum* is one of the most widely distributed genera of the Helenieae, it is not the most primitive. Johnston and Turner (1962) indicated that *Porophyllum* is one of the more recently derived genera of the group, stating that this is hypothetical speculation based largely on chromosome numbers in species of *Porophyllum* and related genera. Small and Johnston (1937) suggested that the genus originated during the late Miocene in Mexico. Distributional patterns indicate to me that the center of distribution, and possibly the center of origin, was either in Mexico or Central America.

SYSTEMATIC TREATMENT

GENERIC DIAGNOSIS

POROPHYLLUM Guett., Acad. Sci. Par., Mem. [1750] 1754.

Cacalia L., Sp. Pl. 834. 1753 (in part).
Kleinia Jacq., Enum. Pl. Carib. 8. 1760.
Hunteria Moc. & Sessé ex DC., Prodr. 5:648. 1836. Not *Hunteria* Roxb. 1814.

Annual or perennial herbs, sub-shrubs, or occasionally large shrubs, glabrous, rarely pubescent, often glaucous; leaves alternate, opposite, or both, simple; blades broad and sinuate with slender petioles to filiform, entire, and sessile with translucent oil-glands along the margins or sometimes also scattered on the surfaces, occasionally lacking; heads homogamous, discoid, borne in cymes, corymbs, panicles, solitary, or 2-several at the ends of branches; involucre cylindric or campanulate, uniseriate; phyllaries 5-9, linear to oblong, ovate or obovate, free or connate only at the base with linear to oblong, dorsal or sub-marginal, translucent oil glands in 2 rows or occasionally a single row; receptacle small, naked; flowers perfect, fertile; corollas whitish, purplish, greenish or yellow, actinomorphic to slightly bilabiate, throat funnelform and several times shorter than the slender tube to cylindric and longer than the tube; anthers rounded to obscurely sagitate at the base, acute at the apex; style branches elongated, subulate, hirtellous; pappus of numerous free bristles, hispidulous or scabrescent; achenes slender, linear to long triangular, striate, often tapering at the apex, usually puberulent, commonly hispidulous, rarely glabrous.

TYPE SPECIES: *Cacalia porophyllum* L.≡*Porophyllum ellipticum* Cass.= *P. ruderale* (Jacq.) Cass.

KEY TO THE SECTIONS

Corolla throat funnelform, two to several times longer than the slender tube; leaf-blades generally thin, broad to filiform; plants of South, Central, and more mesic regions of North America. ..... section *Porophyllum*

Corolla throat funnelform to cylindric, shorter than to several times longer than the tube; leaves thick, sessile, sub-sessile, or short petioled; blades narrow; plants of arid and semi-arid portions of Mexico and the southwestern United States. ..... section *Hunteria*

KEY TO THE SPECIES OF SECTION *POROPHYLLUM*

1. Annuals; leaves petiolate, thin, elliptical, oblong, ovate, or obovate, occasionally widely lanceolate or oblanceolate ..... (2)
1. Perennials; leaves sessile or subsessile, filiform to lanceolate, rarely elliptical (*P. oppositifolium*), or if petiolate and leaves wider, then plants shrubby ..... (7)

2 Phyllaries with 2 even rows of linear glands; peduncles thickened (usually clavate) under the involucre ..... (3)
2. Phyllaries with 1 median row or 2 irregular rows of linear glands; peduncles filiform throughout ..... (5)
3. Achenes longer than 9 mm, or when shorter (*P. leiocarpum*) pappus shorter than achenes; leaves ovate or obovate, apex widely obtuse to rounded; base usually rounded ..... (4)
3. Achenes shorter than 9 mm; pappus longer than achenes; leaves usually elliptical, apex mucronate to obtuse, base usually attenuate ..... 1b. *P. ruderale* subsp. *ruderale*
4. Achenes pubescent, usually longer than 10 mm ..... 1a. *P. ruderale* subsp. *macrocephalum*
4. Achenes glabrous, usually shorter than 10 mm ..... 2. *P. leiocarpum*
5. Phyllaries longer than 14 mm; flowers about 15 or fewer ..... (6)
5. Phyllaries shorter than 14 mm; flowers about 20 ..... 11. *P. calcicola*
6. Flowers about 15; phyllaries acuminate ..... 12. *P. pringlei*
6. Flowers about 5; phyllaries acute ..... 13. *P. quinqueflorum*
7. Herbaceous or suffruticose; leaves filiform to lanceolate or oblanceolate (South America) ..... (8)
7. Shrubs or sub-shrubs; leaf-blades wide, oblong, ovate, elliptical, or obovate (Central America and Mexico) ..... (12)
8. Phyllaries shorter than 15 mm; corollas shorter than 10 mm; phyllary length to width ratio less than 7:1 ..... (9)
8. Phyllaries longer than 15 mm; corollas longer than 10 mm, or if shorter then phyllary length to width ratio greater than 7:1 ..... (10)
9. Plants up to 10 dm high, erect; leaves linear to widely lanceolate or oblanceolate ..... 3. *P. lanceolatum*
9. Plants 2 dm high or less, ascending to erect; leaves filiform to narrowly linear ..... 6. *P. linifolium*
10. Leaves lanceolate or elliptical; phyllaries wider than 2.5 mm ..... (11)
10. Leaves filiform; phyllaries narrower than 2.5 mm ..... 7. *P. angustissimum*
11. Leaves lanceolate, sessile to sub-sessile; phyllaries 20 mm or longer ..... 8. *P. hasslerianum*
11. Leaves elliptical, amplexicaul; phyllaries shorter than 20 mm ..... 9. *P. oppositifolium*
12. Heads nodding; phyllaries thin with 1 median row or 2 scattered rows of linear glands; corollas yellowish or greenish ..... (13)
12. Heads erect or spreading; phyllaries thick with 2 even rows of linear glands, corollas pale to purplish ..... 10. *P. punctatum*
13. Leaves thin; phyllaries of uniform texture and with 2 irregular rows of linear glands ..... 8. *P. nutans*
13. Leaves thick; phyllaries with a thicker, darker dorsal midline bearing 1 row of 2 irregular rows of linear to oblong glands ..... 9. *P. viridiflorum*

KEY TO THE SPECIES OF SECTION *HUNTERIA* (Moc. & Sessé) DC.

Hunteria (Moc. & Sessé, as genus) *ex* DC., Prodr. 5:648. 1836.
Type Species: *Porophyllum linaria* (Cav.) DC.

1. Perennial; phyllaries entirely or not at all glaucous; leaves filiform to lanceolate ..... (2)
1. Annual; phyllaries usually glaucous on distal ⅓; leaves linear to lanceolate (central Mexico) ..... 14. *P. tagetoides*
2. Corollas ochroleucous or white to purple, funnelform, obviously constricted between tube and throat ..... (3)
2. Corollas yellow, cylindric or cylindro-funnelform, not or obscurely constricted between tube and throat ..... (12)
3. Phyllaries purple or when green usually purple tinged; heads solitary or in open inflorescence, if in dense cymes then corallas ochroleucous .... (4)
3. Phyllaries pale green; heads short peduncled, in dense cymes; corollas whitish (maritime plants of Guaymas, Sonora) ..... (11)
4. Leaves linear to lanceolate, oblanceolate, or oblong; heads purple, often with greenish tinge ..... (5)
4. Leaves usually filiform, some plants with leaves partially linear; heads purple to green ..... (7)
5. Heads (especially when immature) usually partially green with purple dots; leaves partially or wholly lanceolate, oblanceolate, or oblong (west & central Mexico) ..... (6)
5. Heads purple or partially green without purple dots; leaves linear (northeastern Mexico) ..... 15. *P. linaria*
6. Corollas dark purple ..... 18. *P. coloratum*
6. Corollas pinkish or whitish ..... 19. *P. obtusifolium*
7. Leaves strictly filiform; plants erect; corollas without orange on lobes .... (8)
7. Leaves partially linear, or if strictly filiform, plants not erect or corollas with orange on lobes ..... (9)
8. Plants covered with minute whitish dots; corollas pinkish-white, longer than 6 mm; phyllaries green to purple tinged ..... 17. *P. warnockii*
8. Plants without whitish dots; corollas purple, shorter than 6 mm, phyllaries dark purple, sometimes with pale margins ..... 16. *P. filiforme*
9. Corollas pale or ochroleucous; leaves filiform to partially linear ..... (10)
9. Corollas purple with slight orange tinge on lobes; leaves long, filiform (southern cape of Baja California) ..... 25. *P. porfyreum*
10. Leaves mostly opposite, fleshy; branches divaricate (southern cape of Baja California) ..... 24. *P. maritimum*
10. Leaves mostly alternate, not fleshy; stems usually erect ..... 23. *P. gracile*
11. Leaves up to 8.5 mm wide, lower ones lanceolate, petiolate ..... 26. *P. brachypodum*
11. Leaves 5.5 mm or less wide, linear to linear-oblanceolate, subsessile ..... 27. *P. pausodynum*
12. Phyllaries 7-10; apices acute to acuminate ..... (13)
12. Phyllaries 5; apices obtuse to rounded ..... (14)
13. Leaves lanceolate, semi-amplexicaul; phyllaries with 4 or more rows of linear glands ..... 20. *P. amplexicaule*
13. Leaves filiform; phyllaries usually with 2 rows of linear glands near mid-line ..... 21. *P. scoparium*

14. Leaves filiform, not crowded on the stem (southwestern Texas) ..... 22. *P. greggii*
14. Leaves linear, crowded on the stem (maritime plants of Baja California)
15. Leaf-apex three cleft; achenes sparsely scabrescent to hispidulous ..... 28a. *P. tridentatum* var. *tridentatum*
15. Leaf-apex simple; achenes sparsely hispidulous to glabrate ..... 28b. *P. tridentatum* var. *crassifolium*

1a. **Porophyllum ruderale** (Jacq.) Cass. subsp. **macrocephalum** (DC.) R. R. Johnson, comb. nov.

Porophyllum macrocephalum DC., Prodr. 5:648. 1836.
Kleinia glandulosa Moc. & Sessé; DC., Prodr. 5:648, pro syn. 1836.
Porophyllum latifolium Benth., Journ. Bot. 2:441. 1840, in part.

Annual, erect, glabrous, somewhat glaucous; stems branching above, 1.5-10 dm high, green to purplish, terete, striate; leaves opposite or alternate, blades 1-3.5 cm long, up to 2.5 cm wide, thin, broadly ovate to obovate, rarely widely lanceolate or oblanceolate, sinuate with one gland in each sinus and one at the apex, surfaces of the blades with or without glands, apex rounded, base usually rounded, sometimes attenuate, petioles 0.5-2 cm long; heads solitary at the ends of branches; peduncles erect, clavate, 1.5-6.4 cm long; phyllaries 5, green, purple tinged, 17-23 mm long, 2.5-3.7 mm wide, linear with 2 rows of linear glands, apex obtuse or acute, rarely acuminate; flowers 30 or more, corolla 9.2-12.4 mm long, puberulent, purple to olive-green, slender tube several times longer than the funnelform throat; pappus 6.7-9.7 mm long, straw-colored to brown, bristles scabrescent; achenes 9.5-12.4 mm long, hispidulous.

Flowering time: Throughout year depending on latitude.

Type: Mexico, near Villalpando (*fide* Rydberg, 1916); photo (KANU! US!).

Distribution: Extreme southwestern United States to northern Brazil, southern Peru, and Bolivia (Fig. 11).

Although previously considered species, both *macrocephalum* and *ruderale* are here considerd subspecies. The distribution of subsp. *macrocephalum* is generally north of subsp. *ruderale*. However, in much of northern South America where the two entities are sympatric, intermediate plants are not uncommon, and they generally have floral characteristics of *macrocephalum* and vegetative characteristics of *ruderale*, but the reverse situation also occurs. A few intermediate specimens are as follows: Curacao. Ronde Klip, 20 Dec 1951, *Arnoldo 1805* (US). Colombia. Antioquia, 9 Oct 1947, *Gutierrez & Barkley 17C075* (US). Venezuela. Near Petare, ca Caracas, 11 Sep 1921, *Pittier 9797* (US). Ecuador. Prov. Guayas, Puntilla, Salinas, 4 Apr 1941, *Svenson 11229* (GH, US). Peru. Prov. Moquegua, between Moquegua and Torata, 21 Mar 1925, *Weberbaur 7429* (GH, MO, US). Bolivia. Cocha-

bamba, Panduro, Mar 1944, *Cardenas 2480* (US). BRAZIL. Cratheus, Ceara, 9-10 May 1934, *Swallen 4501* (GH, US).

Subspecies *ruderale* is common as a weed in low, flat areas, such as fields and vacant lots, through much of its range. It usually is found at elevations below 1,300 m but may occur up to 2,500 m or more. In contrast, subsp. *macrocephalum* occurs more commonly at higher elevations in rocky terrain although it is sometimes found in weedy situations, such as in roadside clearings, and even forms thickets near Progresso, Yucatan (Standley, 1931). In northern Mexico, I have encountered *macrocephalum* most commonly on rough limestone hills.

REPRESENTATIVE SPECIMENS: UNITED STATES. ARIZONA. Santa Cruz Co., Sycamore Canyon, 6 Oct 1962, *Mason 2144* (ARIZ, KANU). TEXAS. Brewster Co., Chisos Mts., 30 Aug 1938, *Warnock C651* (TEX).

MEXICO. BAJA CALIFORNIA. Sierra de la Giganta, s of Tinaja de Naucoyoa and w of Llanos de San Juan, 25 Nov 1962, *Carter 4496* (UC). SONORA. 4½ mi w of Alamos, 5 Nov 1963, *Johnson 2234* (KANU). CHIHUAHUA. Guasaremos, Rio Mayo, 25 Sep 1935, *Gentry 1850* (ARIZ, F, GH, UC). COAHUILA. Canyon del Indio Felipe, Sierra Hechiceros, 27-29 Sep 1940, *Stewart 47* (GH). NUEVO LEON. 12 mi e of Iturbide, 30 Sep 1960, *Crutchfield & Johnston 5838* (TEX). SINALOA. 20 mi n of Culiacán, 6 Nov 1963, *Johnson 2252* (KANU). DURANGO. Durango City and vicinity, Apr-Nov 1896, *Palmer 694* (F, GH, MO, NY, UC, US). SAN LUIS POTOSI. Hills ca Cardenas, 7 Oct 1890, *Pringle 3299* (F, GH, MO, ND, UC, US). NAYARIT. La Atarjea, n of Ixtlán, 1 Oct 1926, *Mexia 883* (GH, NY, UC, US). JALISCO. 76 mi n w of Guadalajara, 7 Nov 1963, *Johnson 2280* (KANU). GUANAJUATO. Guanajuato and vicinity, Sep 1897, *Duges* (GH). QUERÉTARO. 9 mi w of Querétaro, 5 Oct 1955, *Johnston 2900* (SMU, TEX). TAMAULIPAS. 7 mi s of Antiguo Morelos, 28 Oct 1959, *Graham & Johnston 4571* (TEX). VERACRUZ. Jalapa, 18 Aug 1901, *Rose & Hay 6368* (US). MICHOACAN. 2 mi s e of Zamora, 8 Nov 1963, *Johnson 2284* (KANU). MEXICO. Temacaltepec, Chorrera, 10 Sep 1932, *Hinton 2037* (GH, MO, NY, US). MORELOS. Yautepec, 21 Oct 1902, *Pringle 9952* (GH, MO, NY, US). GUERRERO. Temisco, Barranca del Consuelo, 15 Nov 1937, *Mexia 8814* (F, GH, MO, NY). OAXACA. Valley about Cuicatlán, 3 Nov 1894, *Nelson 1876* (US). YUCATAN. Izamal, *Gaumer 2510* (F, GH, NY).

CENTRAL AMERICA. GUATAMALA. Dept. Huehuetenango, between Nenton and las Palmas, 30 Aug 1942, *Steyermark 51614* (F, US). EL SALVADOR. Dept. Santa Ana, ca Metapan, 29 Jan-1 Feb 1947, *Standley & Padilla 3271* (F, US). NICARAGUA. Dept. Managua (about 1930-1940), *Garnier 3* (US). COSTA RICA. Rio Cerbo ca Buenos Aires, Feb 1892, *Pittier 4918* (US). PANAMA. Between Puerto Posada and Penonome, 23 Feb 1908, *Williams 169* (US).

SOUTH AMERICA. COLOMBIA. Dept. Bolivar, n of Arjona, 15 Nov 1926, *Killip & Smith 14551* (F, GH, NY, US). VENEZUELA. Maracáy, *Vogl 656* (US). ECUADOR. Prov. Guayas, Punta Centinela, 6 Apr 1941, *Svenson 11261* (NY, US). GALAPAGOS ISLANDS. Albermarle Is., Tagus Cove, 27 Mar 1906, *Stewart 656* (GH, MO, NY, US). PERU. 56 km e of Lima (16 km e of Chosica), Río Rimac Canyon, 24 Mar 1952, *Hutchison 541* (US). BOLIVIA. Cochabamba, Cerro de San Pedro, 18 Mar 1939, *Balls 6293* (US). BRAZIL. Rio Branco, Surumu, Aug 1909, *Ule 8356* (US). BRITISH GUIANA. Rupununi River, *Forest Dept. WB 77* (NY).

1b. **Porophyllum ruderale** (Jacq.) Cass. subsp. **ruderale**

Cacalia porophyllum L., Sp. Pl. 834. 1753.
Kleinia ruderalis Jacq., Enum. Pl. Carib. 28. 1760.
Cacalia ruderalis Sw., Prodr. 110. 1788.
Cacalia glandulosa Salisb., Prod. 187. 1796.
Kleinia porophyllum Willd., Sp. Pl. 3:1738. 1804.
Porophyllum ellipticum Cass., Dict. Sci. Nat. 43:56. 1826.
Porophyllum ruderale Cass., Dict. Sci. Nat. 43:56. 1826.
Porophyllum ellipticum β. intermedium DC., Prodr. 5:648. 1836.
Porophyllum latifolium Benth., Journ. Bot. 2:441. 1840, in part.

Porophyllum porophyllum Kuntze, Rev. Gen. 3(2):168. 1898.
Porophyllum macrolepideum Malme, Kgl. Sv. Vet. Akad. Handl. 32(5):69. 1899.
Porophyllum ellipticum var. *genuinum* Urb., Symb. Ant. 1:467. 1900.
Porophyllum ellipticum var. *ruderale* Urb., Symb. Ant. 1:468. 1900.
Porophyllum ruderale f. *suffruticosa* Chod., Bull. Herb. Boiss. Ser. 2, 3:729. 1903.
Porophyllum ruderale var. *macrolepideum* Chod., Bull. Herb. Boiss. Ser. 2, 3:729. 1903.
Porophyllum ruderale var. *glandulosum* Chod., Bull. Herb. Boiss. Ser. 2, 3:729. 1903.
Porophyllum ruderale var. *angustifolia* Hassl., Trab. Mus. Farm. Fac. Cienc. Med. Buenos Aires 21:131. 1909.
Porophyllum ruderale var. *ellipticum* Robins., Prod. Am. Acad. 49:509. 1913.
Tagetes integrifolia Musch., Engl. Bot. Jahrb. (50 Beibl.) 111:77. 1913.

Blades 1-6 cm long, up to 30 mm wide, thin, elliptical, rarely ovate or obovate, rarely with glands scattered on the surface or without glands, apex mucronate to obtuse, base usually attenuate, sometimes acute, rarely obtuse; peduncles usually slightly to moderately clavate; phyllaries 16-22.5 mm long, 2-3 mm wide, apex acuminate; corolla 8.2-13.5 mm long; pappus 9-11.5 mm long, light to dark straw-colored; achenes 8.1-8.9 mm long.

Flowering time: Throughout year depending on latitude.

Type: Photo (KANU! US!).

Distribution: Throughout tropical America; Costa Rica and the West Indies, south to southern Peru, and through Brazil into northern Argentina (Fig. 12). See discussion under *P. ruderale* subsp. *macrocephalum*.

Representative specimens: WEST INDIES. ABACO. Great Cistern, 19 Dec 1904, *Brace 1764* (F, NY, US). CUBA. Prov. Oriente, Ensanada de Mora, 26-29 Mar 1919, *Britton, Cowell & Shaffer 13067* (F, NY, US). HAITI. Near Jean Rabel, 9 Feb 1929, *Leonard & Leonard 18076* (NY, US). DOMINICAN REPUBLIC. Near Puerta Plata, 15 Jul 1948, *Jimenez 1690* (US). PUERTO RICO. Utuado, 15-20 Mar 1906, *Britton & Cowell 1029* (F, US). ANTIGUA. Cumming Valley, 15 Aug 1937, *Box 971* (US). TRINIDAD. Diego Martin, 27 July 1920, *Broadway* (F, GH, MO, NY, US).

CENTRAL AMERICA. COSTA RICA. Valley of Reventazon, Las Lomas, Aug 1895, *Pittier 9746* (US). PANAMA. Near Fort Lorenzo, Mouth of Rio Chagres, 8 Mar 1923, *Piper 5927* (US).

SOUTH AMEDICA. COLOMBIA. Dept. Huila, Gigante, 3 Jul 1926, *Woronow & Juzepczuk 5593* (US). VENEZUELA. State of Trujillo, ca Valera, 27 May 1944, *Steyermark 56758* (F, US). ECUADOR. Prov. Guayas, 8 mi s of Milagro, 11-13 Jul 1923, *Hitchcock 20578* (GH, NY, US). PERU. Dept. Loreto, Lower Rio Huallaga, Oct-Nov 1929, *Williams 5320* (F, GH, US). Ambo, 5 Apr 1923, *Macbride 3200* (GH, NY, US). BOLIVIA. Mapiri, May 1886, *Rusby 1697* (F, GH, MICH, MO, NY, US). BRAZIL. Para, Rio Tapajos, Boa Vista, 7-13 Jan 1934, *Swallen 3122* (F, NY, US). Parana, Iacarchy, 18 Mar 1914, *Jonsson 87a* (NY, US). Minas Gerais, Vigosa, 25 Feb 1930, *Mexia 4402* (F, GH, MO, NY, US). São Paulo, Poa, 11 Mar 1922, *Holway & Holway 1625* (US). Rio Grande do Sul, Canoas, 1 Feb 1949, *Luis 16* (F, US). PARAGUAY. Caballero, 20 Jan 1889, *Morong 475* (NY, US). ARGENTINA. Prov. Jujuy, San Pedro de Jujuy, 31 May 1943, *Bartlett 20306* (GH, US). Prov. Cordoba, Dept. Punilla, Molinari, 18 Apr 1947, *Gutierrez 152* (US).

2. **Porophyllum leiocarpum** (Urban) Rydb., N. Amer. Fl. 184. 1916.

Porophyllum macrocephalum var. *leiocarpum* Urban, Symb. Ant. 1:466. 1900.

Annual, erect, glabrous, often glaucous; stems branching above, 2-5 cm high, green to purplish, terete, striate; leaves opposite or alternate, blades 1-4 cm long, up to 21 mm wide, ovate, thin, sub-entire to sinuate with 1 oblong gland in each sinus and 1 at the rounded apex, base usually rounded, sometimes attenuate, petioles 0.5-2 cm long; heads solitary at the ends of

branches; peduncles erect, slightly clavate, 1.2-4.5 cm long; phyllaries 5, green, purple tinged, 19-20.2 mm long, 1.7-2.9 mm wide, linear, with 2 rows of linear glands, apex acute; flowers 30 or more, corolla 10-11.4 mm long, puberulent, purple to olive green, slender tube several times longer than the funnelform throat; pappus 7-9.1 mm, straw-colored to brown, bristles scabrescent; achenes 8.6-10.1 mm long, glabrous.

Flowering time: Throughout year.

Type: Puerto Rico. 2 Feb 1886, *Sintenis 3576* (NY!).

Distribution: Puerto Rico and seacoasts of South America where it undoubtedly has been introduced as a weed (Fig. 12).

This entity is retained as a species rather than as a variety of *P. macrocephalum*. Specimens from Puerto Rico show no signs of intergradation or hybridization of *P. leiocarpum* with *P. ruderale* subsp. *ruderale*, which occurs in the same area. Furthermore, there is no indication of hybridization with *P. ruderale* subsp. *macrocephalum* on the South American mainland where both *P. leiocarpum* and *macrocephalum* occur.

Representative specimens: PUERTO RICO. Bayamon, Aibonito, 14 Nov 1937, *Otero 281* (GH, MICH). On Adjuntas Road, 11 mi from Ponce, 31 Dec 1902, *Heller 6359* (F, GH, MO, NY, US). VENEZUELA. Near Petare, ca Caracas, 1 Sep 1921, *Pittier 9797* (US). Caracas, 6 Dec 1938, *Alston 5361* (NY, US). PERU. Cerro Prieto, Piura, 31 Mar 1929, *Haught 233* (GH, NY, US). BRAZIL. Sao Paulo, 10 Sep 1920, *Hoehne 16875* (US).

3. **Porophyllum lanceolatum** DC., Prodr. 5:649. 1836.

Kleinia obscura Spreng., Syst. 3:438. 1826.
Kleinia linifolia Gill. & Don *ex* Hook. & Arn., Comp. Bot. Mag. 2:52. 1836.
Porophyllum prenanthoides DC., Prodr. 5:649. 1836.
Porophyllum haenkei DC., Prodr. 5:649. 1836.
Porophyllum lineare DC., Prodr. 5:649. 1836.
Porophyllum obscurum DC., Prodr. 5:651. 1836.
Porophyllum martii Baker *in* Mart., Fl. Bras. 6(3):284. 1884.
Porophyllum exsertum Baker *in* Mart., Fl. Bras. 6(3):284. 1884.
Porophyllum oblanceolatum Rusby, Mem. Torr. Bot. Club 6:64. 1896.
Porophyllum lineare f. *latifolia* Chod., Bull. Herb. Boiss. Ser. 2, 2:397. 1902.
Porophyllum lineare var. *corymbosum* Chod., Bull. Herb. Boiss. Ser. 2, 2:397. 1902.
Porophyllum lanceolatum f. *foetens* Chod., Bull. Herb. Boiss. Ser. 2, 3:729. 1903.
Porophyllum lanceolatum var. *angustius* Chod., Bull. Herb. Boiss. Ser. 2, 3:729. 1903.
Porophyllum lanceolatum var. *induratum* Chod., Bull. Herb. Boiss. Ser. 2, 3:730. 1903.
Porophyllum lanceolatum var. *corymbosum* Chod., Bull. Herb. Boiss. Ser. 2, 3:730. 1903.
Porophyllum lanceolatum f. *depauperata* Chod., Bull. Herb. Boiss. Ser. 2, 3:730. 1903.
Porophyllum lanceolatum var. *genuinum* Hass. in Fedde, Rep. Spec. Nov. 16:28. 1919.
Porophyllum lanceolatum var. *lineare* Hass. in Fedde, Rep. Spec. Nov. 16:29. 1919.
Porophyllum lanceolatum var. *glaucum* Hass. in Fedde, Rep. Spec. Nov. 16:29. 1919.
Porophyllum curticeps Malme, Arkiv. Bot. 24 A(6):74. 1932.
Porophyllum eremophilum Cabrera, Darwiniana 9:43. 1949.

Perennial, glabrous, often glaucous; stems erect, up to 10 cm high, green to purple, becoming brown to brownish-purple with age, terete, rigid, striate; leaves opposite or alternate, sessile to short petioled, up to 5 cm long and to 17 mm wide, narrowly linear to widely lanceolate or oblanceolate, marginal glands variable in number; heads borne in panicles or solitary on the ends of

branches; peduncles 1-7 cm long; phyllaries 5, greenish to purple, 10.8-14.5 mm long, 1.6-3 mm wide, linear to oblanceolate with 2 rows of linear glands, apex acute; corolla 6-8.7 mm long, pale to dark purple or olive green, tube much longer than the funnelform throat; pappus 5.8-8.2 mm long, straw-colored to purplish, bristles hispidulous; achenes 5-8.2 mm long, hispidulous.

Flowering time: Throughout year.

Type: Brazil. *Gaudichaud 936*. Photo (US!).

Distribution: Bolivia, northern Argentina, Paraguay, and southern Brazil (Fig. 13).

This is the most variable species of *Porophyllum* in South America, equaling or surpassing in variation *P. gracile* of North America. Leaves are either opposite, alternate, or both, and vary gradually from narrowly linear to widely lanceolate or oblanceolate. It is impractical to divide a complete series of *P. lanceolatum* into varieties by vegetative characters alone. Specimens of DeCandolle's *P. prenanthoides* without the wide lower leaves are indistinguishable from *P. lanceolatum*. In addition, glaucous specimens from Brazil (Rio Grande do Sul) which could be placed in *P. lanceolatum* var. *glaucum* (Paraguay) sometimes have leaves as large as *P. prenanthoides* (*sensu* DeCandolle), which is not glaucous.

Glaucous specimens from Argentina, which do not fit Hassler's variety *glaucum* but do fit *P. lanceolatum* vegetatively, approach *P. ruderale* in head characteristics. Non-glaucous specimens from Paraguay with leaf and stem characteristics of *P. lanceolatum* also approach *P. ruderale* in head characteristics.

Porophyllum hasslerianum and *P. linifolium* are morphologically closely allied to *P. lanceolatum*. The leaves of *P. linifolium* are shorter than those of *P. hasslerianum* and, although there is some overlap between those of *P. hasslerianum* and *P. lanceolatum*, those of *P. hasslerianum* are generally longer. All head measurements of *P. hasslerianum* are much larger than those of either *P. lanceolatum* or *P. linifolium*. Hybridizations, cytogenetic analysis, and further collecting may result in the confirmation of conspecific status for *P. hasslerianum* and *P. lanceolatum*.

Specimens of *P. linifolium* are usually ascending in contrast to the erect habit of both *P. lanceolatum* and *P. hasslerianum*. In addition the leaves of *P. linifolium* are generally filiform and shorter than those of *P. lanceolatum*. However, certain specimens, particularly from Argentina, resemble *P. lanceolatum* in having nearly erect stems and narrowly linear leaves. These specimens, however, have the typically short stems of *P. linifolium*, and short, wide phyllaries with apices obtuse (in contrast to the acute apices of *P. lanceolatum*).

Representative specimens: BOLIVIA. Charagua, Apr 1934, *Cardenas 2609* (US). Below Cochabamba, 1891, *Bang Lectae 1013* (NY, US). ARGENTINA. Prov. Tucumán, Capital, Río Salí, 5 May 1920, *Venturi 814* (US). Prov. Mendoza, Barrancas, 12 Jan 1943,

Bartlett 19342 (US). Prov. Corrientes, ca Perugórria, 12 Dec 1957, *Pedersen 4688*. PARAGUAY. Pilcomayo River, 1888-1890, *Morong 889* (F, GH, US). In region Yhu River, Nov 1905, *Hassler 9671* (GH, US). BRAZIL. Minas Gerais, 11 May 1931, *Mexia 5807* (GH, US). Parana, between Juho de Castillo and Jaquariahyva, 21 Nov. 1914, *Dusen 16016* (F, GH, US). Rio Grande do Sul, 21 Nov 1904, *Bornmuller 347* (GH).

4. **Porophyllum hasslerianum** Chodat, Bull. Herb. Boiss. II, 3:730. 1903.

Perennial, suffruticose; stem erect, green, purple tinged, terete, striate to angled; leaves opposite or alternate, subsessile, 4.5-8 cm long, 5.5-10 mm wide, lanceolate, acute, base attenuate, marginal glands small, up to 30 per leaf; heads solitary at the ends of branches; peduncles elongate, widely inflated below the involucre, up to 13.3 cm long; phyllaries 5, greenish-purple, 20-22 mm long, 4-4.5 mm wide, linear-lanceolate with 2 rows of linear glands, apex sharply acute to acuminate; flowers more than 40, corolla 14.3-15.1 mm long, purple, tube several times as long as the narrowly funnelform throat; pappus 9.9-10.8 mm long, straw-colored, bristles hispidulous; achenes *ca.* 10-11 mm long, hispidulous.

FLOWERING TIME: November and December.

TYPE: Paraguay. In the region around the upper Apa River, Nov-Dec 1901, *Hassler 8086* (NY! US!).

DISTRIBUTION: Paraguay (Fig. 13).

This species is most closely related to *P. lanceolatum* and is discussed under that species.

5. **Porophyllum oppositifolium** Ktze., Rev. Gen. 3(2):168. 1898.

Porophyllum platyphyllum Chod., Pl. Hassl. 1:168. 1902.

Perennial, glabrous, glaucous; stem herbaceous, erect, stout, up to 8 dm high, green to brownish-purple, terete, striate; leaves opposite, coriaceous, up to 6.7 cm long, 32 mm wide, elliptical, sinuate, marginal glands widely linear, up to 30 or more per leaf, apex acute to obtuse, base amplexicaul; peduncles numerous, borne in leaf axils, erect 3.5-8.4 cm long, greatly thickened at the base of the head; phyllaries 5, green, purple tinged, 15.8-19.4 mm long, 3.4-4 mm wide, linear-lanceolate, acute, with 2 rows of linear glands; flowers more than 60; corollas 10.8-13.8 mm long, purple, hispidulous, the lighter tube several times longer than the dark funnelform throat; pappus 8.7-10.3 mm long, straw-colored to purple tinged, bristles hispidulous; achenes 7.5-9.6 mm long, hispidulous.

FLOWERING TIME: December through February (data incomplete).

TYPE: Brazil(?). Mattogrosso (=Mato Grosso), *Kuntze* (NY!).

DISTRIBUTION: Paraguay and probably adjacent Brazil (Fig. 13).

REPRESENTATIVE SPECIMENS: PARAGUAY. Cordillera de Altos, Feb, *Hassler 3907* (F, GH, US). In the region around the upper Apa River, Dec, *Hassler 8070* (F, GH, MO, NY, US).

6. **Porophyllum linifolium** (L.) DC., Prodr. 5:649. 1836.

Cacalia linifolia L., Mant. 109. 1767.
Kleinia suffruticosa Willd., Sp. Pl. 3:1739. 1804.
Cacalia linaria var. *pumila* Poir., Suppl. 2:6. 1811.
Kleinia filifolia Spreng., Syst. 3:438. 1826.
Kleinia pumila Hook. & Arn., Comp. Bot. Mag. 2:52. 1836.
Porophyllum filifolium DC., Prodr. 5:651. 1836.

Perennial, herbaceous, glabrous, sometime glaucous; stems ascending to erect, 1-2 dm high, green to purple tinged, terete, striate; leaves alternate, 1-3.5 cm long, filiform to narrowly linear, revolute, with several small oblong glands; heads solitary at the ends of branches; peduncles 1.5-6 cm long, slightly enlarged at the base of the involucre; phyllaries 5, green to purple, 9-13 mm long, 2.3-4 mm wide, linear-oblanceolate, with 2 rows of linear glands, apex acuminate to obtuse; flowers *ca.* 40, corolla 7.1-8.6 mm long, pale to dark purple, puberulent, tube much longer than the funnelform throat; pappus 5-6.1 mm long, straw-colored to purple tinged, bristles hispidulous; achenes 5-7.4 mm long, hispidulous.

Flowering time: October through January.

Type: South America. Photograph of type from Linnaean Herbarium examined (KANU!).

Distribution: Uruguay and adjacent Argentina and Brazil (Fig. 13).

Relationships between *P. linifolium* and the closely allied *P. lanceolatum* and *P. hasslerianum* are discussed under *P. lanceolatum*.

Representative specimens: ARGENTINA. Near San Francisco del Chanar, Córdoba, 9 Jan 1920, *Kuntze* (NY, US). BRAZIL. Sello, 385 (GH). Porto Alegre, 10 Oct 1910, *Malme 120B* (GH). URUGUAY. Dept. Paysandu, n of Quebracho, 9 Dec 1943, *Bartlett 21171*. Dept. Montevidéo, Carrasco, 20 Nov 1910, *Osten 5336*.

Porophyllum linifolium var. **brevifolium** (Hook. & Arn.) Baker, in Mart., Fl. Bras. 6(3):283. 1884.

Kleinia brevifolia Hook. & Arn., Comp. Bot. Mag. 2:52. 1836.
Porophyllum decumbens DC., Prodr. 5:650. 1836.
Porophyllum brevifolium Malme, Kgl. Sv. Vet. Akad. Handl. 32(5):70. 1899.

This variety is known only as a cultivar. Although it reportedly came from Mexico, it is obviously a wide-leafed variety of *P. linifolium* (Robinson, 1914). Furthermore, the variety passed out of cultivation and is now known only from a few herbarium specimens, in addition to drawings. A specimen examined (GH) had leaves up to 2.3 cm long and 4 mm wide.

7. **Porophyllum angustissimum** Gardn., Lond. Journ. Bot. 7:410. 1848.

Kleinia filifolia Hook. & Arn., Comp. Bot. Mag. 2:52 (in part). 1836; not *K. filifolia* Spreng., Syst. 3:438. 1826.
Porophyllum riedelii Schultz Bip. *ex* Baker *in* Mart., Fl. Bras. 6(3):284. 1884.
Porophyllum arenosum Schultz Bip. *ex* Baker *in* Mart., Fl. Bras. 6(3):285. 1884.

Perennial, herbaceous, glabrous; stem erect, branching above, 2-6 dm high, greenish brown to purple, terete, striate; leaves alternate, 2-5 cm long, filiform; heads borne in open panicle; peduncles 4-15 mm long; phyllaries 5, purplish, 15-18 mm long, 1.8-2.4 mm wide, linear-lanceolate, acute, with 1-2 rows of long linear glands, sometimes each gland running entire length of bract; flowers *ca.* 15, corolla 8-10.6 mm long, purplish, tube scabrous, several times as long as the narrowly funnelform throat; pappus 7.3-11 mm long, dark straw to brown, bristles hispidulous; achenes 5.7-7.6 mm long, finely hispidulous.

FLOWERING TIME: June (data incomplete).

TYPE: Brazil. Prov. Goyaz (=Goias), *Gardner 4259* (F! NY! US!).

DISTRIBUTION: Southern Brazil (Fig. 13).

REPRESENTATIVE SPECIMENS: BRAZIL. Matto Grosso, Santa Anna, 4 Jun 1903, *Malme 2005* (GH). *Riedel* (US).

8. **Porophyllum nutans** Robins. & Greenm., Proc. Amer. Acad. 32:31. 1896.

Porophyllum holwayanum Greenm., Proc. Amer. Acad. 40:48. 1904.

Shrub up to 3 m high, glabrous; stem profusely branched, yellowish-green becoming reddish brown with age, terete, striate; leaves mostly opposite, blades thin, ovate or elliptical, usually sinuate with up to 9 oblong glands, 1 in each sinus, and 1 at the acute to rounded apex, base obtuse or acute, petioles slender, 5-18 mm long; heads nodding, numerous, in leafy clusters at the ends of branches; peduncles slender, 1-3 cm long; phyllaries 5, yellowish-green, 14.7-16 mm long, 1.5-2.8 mm wide, linear, thin, obtuse, with 2 rows of scattered linear glands; flowers *ca.* 20, corolla yellowish or greenish, 8.2-10 mm long, tube much longer than the funnelform throat; pappus 7.8-9.1 mm long, straw colored, bristles hispidulous; achenes 6.3-8.9 mm long, hispidulous.

FLOWERING TIME: October through December.

TYPE: Mexico. Michoacan. Mountains near Lake Chapala, 16 Dec 1889, *Pringle 2976* (NY!); isotypes (F! MO! US!).

DISTRIBUTION: Jalisco south through Guerrero and inland to Hidalgo and Morelos (Fig. 14). See discussion under *P. viridiflorum*.

REPRESENTATIVE SPECIMENS: MEXICO. JALISCO. Chapala, 5 Oct 1903, *Rose & Painter 7652* (GH, US). MICHOACAN. Cerro Potrerillos, ca 5 mi n of Cotija, 22 mi s of Jiquilpán, 5-8 Oct. 1961, *King & Soderstrom 4658* (MICH, SMU). HIDALGO. Jacala, 17 Nov 1937, *Kenover 616* (F). MEXICO. Dist. Temascaltepec. Ixtapan, 19 Oct 1932, *Hinton 2241* (MO, NY, US). MORELOS. Coronilla, 19 Sep 1909, *Arsene 42* (F). GUERRERO. 5 mi n of Chilpancingo, 4 Nov 1960, *Crutchfield & Johnston 6001* (MICH, US).

9. **Porophyllum viridiflorum** (HBK) DC., Prodr. 5:648. 1836.

Kleinia viridiflora HBK, Nov. Gen. & Sp. 4:157. 1820.
Porophyllum lindenii Schultz-Bip. *in* Seem., Bot. Voy. Herald 308. 1857.
Porophyllum rotundifolium M. E. Jones, Contr. W. Bot. 18:81. 1933.
Porophyllum purpureum M. E. Jones, Contr. W. Bot. 18:81. 1933.

Shrub up to 2 m or more high, more or less sclerophyllous, glabrous, sometimes glaucous; stem profusely branched, yellowish-green becoming reddish brown with age, terete, striate; leaves opposite or alternate, blades ovate or obovate, up to 5 cm long, 36 mm wide, usually reticulate, subentire, occasionally sinuate with a few marginal glands, 1 in each sinus and 1 at the acute to rounded apex, petioles 0.7-1 cm long; peduncles erect, slender, 0.5-2 cm long; heads solitary or in bracteate clusters at the ends of branches; phyllaries 5, yellowish-green, 12.1-14.2 mm long, 2-2.6 mm wide, linear, thin, obtuse, with 1 row of median oblong glands or 2 rows of scattered linear to oblong glands, often converging into 1 medidan row; flowers *ca.* 20, corolla pale yellow or greenish, 8.1-9.6 mm long, tube hispidulous, much longer than the funnelform throat; pappus 6.5-7.3 mm long, straw-colored, bristles hispidulous; achenes 7-9.4 mm long, hispidulous.

FLOWERING TIME: Throughout year.

TYPE: Mexico. *Bonpland 4297,* fragment (F!).

DISTRIBUTION: Nayarit south through Oaxaca and east to San Luis Potosí and Veracruz (Fig. 14).

Most specimens of *P. viridiflorum* can be distinguished from *P. nutans* without difficulty. However, some of the specimens of *P. viridiflorum* whose leaves have sinuate margins are difficult to separate from *P. nutans.* The most constant character for *P. viridiflorum* is the thicker, darker dorsal mid-line (bearing the glands) on the phyllaries. This contrasts with the very thin margins, giving the phyllaries a keeled appearance.

REPRESENTATIVE SPECIMENS: MEXICO. NAYARIT. Tepic, 5 Jan-6 Feb 1892, *Palmer* (US *305402*). JALISCO. About 15 mi s e of Autlán, trail to El Cuarton, 16 Apr 1949, *McVaugh 10335* (MICH, US). SAN LUIS POTOSI. 15-16 mi e of Ciudad del Maíz, 20 Sep 1960, *Crutchfield & Johnston 5666.1* (TEX). MICHOACAN. Uruapan, 24 Jan 1907, *Pringle 13906* (F, GH, MICH, MO, US). MEXICO. Temascaltepec, 12 Aug 1933, *Hinton 5315* (MO, NY). MORELIA. Xochitepec, Dec 1934, *Lyonnet 815* (US). GUERRERO. Between Tlalixtoquilla and Tlapa, 12 Dec 1894, *Nelson 2096* (US). VERACRUZ. Fortín, ca San Martin Tlacotepec, Apr 1930, *Purpus 15033* (F, MICH, MO, UC). OAXACA. Sierra San Felipe, 11 Nov 1903, *Holway 65* (US).

10. **Porophyllum punctatum** (Mill.) Blake, Contr. Gray Herb. 52:58. 1917.

Eupatorium punctatum Mill., Gardn. Dict. ed. 8, no. 11. 1768.
Kleinia jorullensis HBK, Nov. Gen. & Sp. 4:156. 1820.
Porophyllum nummularium DC., Prodr. 5:649. 1836.
Porophyllum jorullense Cass., Dict. Sci. Nat. 43:57. 1826.
Porophyllum ervendbergii Gray, Proc. Amer. Acad. 19:35. 1883.
Porophyllum palmeri Rose, Contr. U.S. Nat. Herb. 1:338. 1895.
Porophyllum nelsonii Robins. & Greenm., Proc. Amer. Acad. 32:32. 1896.
Porophyllum millspaughii Robins. *in* Millsp., Field Columb. Mus. Publ. Bot. 2:109. 1900.
Porophyllum oblongum Rydb., N. Amer. Fl. 34:186. 1916.
Porophyllum divaricatum Rydb., N. Amer. Fl. 34:186. 1916.
Porophyllum pittieri Rydb., N. Amer. Fl. 34:188. 1916.
Porophyllum guatemalense Rydb., N. Amer. Fl. 34:190. 1916.

Shrub, glabrous; stems much branched, usually 1-2 m high, occasionally to 4 m, greenish to brownish-purple, terete, striate; leaves mostly opposite,

blades 1-3 cm long, 0.6-2.4 cm wide, shape variable, oblong, ovate, or elliptical, sinuate, usually with 2-7 marginal glands on each side and 1 terminal on the acute to rounded apex, sometimes with glands scattered on the surfaces, base rounded to attenuate, petioles 0.4-1.2 cm long; peduncles 0.8-3.5 cm long, ascending or erect, generally spreading, especially with age; heads cymose to corymbose; phyllaries 5, green, yellowish to purplish tinged, 9.3-14.6 mm long, 1.4-2.6 mm wide, linear, acute, with 2 rows of linear glands; flowers 15-30, corolla 6-10.1 mm long, pale to purple, tube equal to longer than the funnelform throat; pappus 6-8.5 mm long, straw-colored to purplish, bristles hispidulous; achenes 6-8.1 mm long hispidulous.

FLOWERING TIME: Throughout year, depending on rain.

TYPE: Sketch of the type (GH!).

DISTRIBUTION: Coastal states of western and eastern Mexican mainland, south through Costa Rica (Fig. 15).

Local populations of this species, located in hilly areas separated from one another by lowlands, apparently have differentiated to such an extent that certain populations have been designated as separate species in the past. In addition, there is tremendous variation in size of the plants. Those in the drier areas of Mexico usually attain a height of one to two meters while plants in southern Mexico, and more mesic regions, attain heights of about four meters (Millspaugh, 1896).

Rydberg (1916) depended on position of glands on the leaves (marginal glands only versus both marginal and surface glands) to separate "species" of this group. However, plants grown in the University of Kansas experimental greenhouse from achenes from a single head show the following variation: plants with very few leaves having surface glands, plants with a large percentage of leaves having glands on the surfaces of the leaves as well as the margin; and plants with nearly all of the leaves having both marginal and surface glands.

Greater variation is often found among individuals of a single species, *sensu* Rydberg, than between type specimens of two or more of his species. These factors combined with a continuous geographic and ecological distribution dictate that these shrubs be considered members of one species.

REPRESENTATIVE SPECIMENS: MEXICO. SINALOA. Cerro Colorado, 27 Nov 1939, *Gentry 5075* (F, GH, MICH, MO, UC, US). Near Mazatlán, Dec 1888, *Wright 1223* (GH, UC). NAYARIT. Punta Mita, 22 Jul 1932, *Howell 10393* (US). JALISCO. Road from Barra de Navidád to Tequezauitlan & Autlán, 8 Apr 1951, *McVaugh 11886* (MICH). COLIMA. Playa de Santiago, n w of Manzanillo, 22 Jul 1957, *McVaugh 15636* (MICH). MICHOACAN. Acahuato, ca Apatzingán, 14 Aug 1941, *Leavenworth & Hoogstraal 1552* (F). GUERRERO. 2 mi w of Colotlipa, 24 Jun 1953, *Hubricels & Rowell 3735* (SMU). OAXACA. Tomellín, 4-5 Sep 1905, *Rose, Painter & Rose 10058* (GH, US). VERACRUZ. Jalapa, 16 Feb 1910, *Orcutt 3163* (GH). CAMPECHE. Champotón, 7-15 Jul 1932, *Steere 1960* (F, MICH, UC). YUCATAN. Chichen Itza, 16 Jun 1932, *Steere 1331* (MICH, US).

CENTRAL AMERICA. HONDURAS. Dept. Yoro, ca Progreso, 24 Jan 1928, *Standley 55056* (US). GUATEMALA. Dept. Zacapa, ca Santa Rosalia, 9 Jan 1942, *Steyermark 42261* (US). EL SALVADOR. Near Santa Ana, 28-30 Jan 1922, *Standley 20422* (GH, NY, US). COSTA RICA. Between Bagaces and Canyas, 29 May 1932, *Brenes 15602* (F).

11. **Porophyllum calcicola** Robins. & Greenm., Proc. Amer. Acad. 39:116. 1903.

Annual, glabrous, somewhat glaucous; stem erect, profusely branched, green to purple tinged, terete, slightly striate; lower leaves opposite, becoming alternate above, blades up to 3.1 cm long, 13 mm wide, oblong to obovate, glands marginal, brown, oblong, 3-7 with 1 at the rounded to obtuse apex, base cuneate, petiole 0.5-2.4 cm long; peduncles erect 1-3 cm long, thickened below the involucre; phyllaries 5, green to purple, 12.3-13.5 mm long, 1.8-2 mm wide, linear, acute, with 1-2 median rows of scattered, linear glands; flowers *ca.* 20, corolla 7-7.3 mm long, tube pale, several times longer than the purple funnelform throat; pappus 5-6.3 mm long, straw-colored, bristles hispidulous; achenes 6.2-6.5 mm long, hispidulous.

Flowering time: October and November.

Type: Mexico. Syntype-Morelos, Yautepec, on limestone hills, 8 Nov 1902, *Pringle 8720* (ARIZ! F! GH! MO! NY! SMU!).

Distribution: Morelos and Guerrero (Fig. 16).

Representative specimens: MEXICO. Morelos. Near Yautepec, 21 Nov 1903, *Pringle 11564* (F, MICH, SMU). Guerrero. Iguala, 3 Nov 1903, *Holway 41* (US). Rio Balsas, 20 Oct 1914, *Seler 4287* (US).

12. **Porophyllum pringlei** Robins., Proc. Amer. Acad. 27:178. 1892.

Annual, glabrous, somewhat glaucous; stem slender, 1.5-6 dm high, branching above, green, terete, striate; leaves mostly opposite, blades thin, up to 4.1 cm long, 13 mm wide, elliptical or oblong, brown marginal glands 0-7 with 1 at the obtuse to rounded apex, base attenuate, petioles 0.8-2.4 cm long; peduncles erect, 0.5-1.7 cm long; phyllaries 5, green, 15.8-18.2 mm long, 1.1-2.1 mm wide, narrowly linear, acuminate, with 1 median row of linear glands; flowers *ca.* 15, corolla 7.1-8.5 mm long, pale tube several times longer than the funnelform throat; pappus 6.9-8 mm long, straw colored, bristles hispidulous; achenes 6.8-8.5 mm long, hispidulous.

Flowering time: September through November.

Type: Mexico. Jalisco. Barranca near Guadalajara, 26 Sep 1889, *Pringle 2954* (GH!).

Distribution: Mexican states of Jalisco, Mexico and Guerrero (Fig. 16).

Representative specimens: MEXICO. Jalisco. Barranca de Guadalajara, 12 Oct 1895, *Pringle 6151* (F, GH, MO, NDG, NY, UC, US). Mexico. Sahtre, 15 Nov 1932, *Hinton 2601* (MO, NY, US). Guerrero. Temisco, Barranca del Consuelo, 15 Nov. 1937, *Mexia 8815* (ARIZ, F, LL, MO, UC, US).

13. **Porophyllum quinque-florum** Brandg., Zoe 5:225. 1905.

Annual, glabrous; stem erect, up to 5 or 6 dm high, profusely branched, divaricate, green to purple tinged, terete, striate; leaves mostly alternate,

blades thin, up to 4 cm long, 15 mm wide, obovate to widely oblanceolate, mostly entire, glands marginal, oblong, brown, 0-7 with 1 at the obtuse to rounded apex, base attenuate, petioles 1-1.7 cm long; peduncles borne in the axils of leaves, spreading, 1-2 cm long; phyllaries 5, green, 16.1-17 mm long, 1.1-1.3 mm wide, narrowly linear, acute, with 1 median row of linear glands; flowers *ca.* 5, corolla *ca.* 8.6 mm long, pale, several times longer than the funnelform throat; pappus 7-7.7 mm long, straw-colored, bristles hispidulous; achenes 7.3-7.7 mm long, hispidulous.

FLOWERING DATE: October.

TYPE: Mexico. Sinaloa. Cerro Colorado, 28 Oct 1904, *Brandegee* (UC!); isotype (US!).

DISTRIBUTION: Known only from the type collection (Fig. 16).

This species is morphologically very close to *P. pringlei*, with the exceptions noted in the key. These differences, combined with the geographic separation from *P. pringlei* and the morphologically nearest species, *P. calcicola*, justify retention of specific rank, at least until further experimental studies can be conducted.

14. **Porophyllum tagetoides** (HBK) DC., Prodr. 5:650. 1836.

Kleinia tagetoides HBK, Nov. Gen. & Sp. 4:158. 1820.
Hunteria fuscata Moc. & Sessé *ex* DC., Prodr. 5:650 (as synonym of *Porophyllum coloratum*). 1836.

Annual, glabrous, rarely glaucous; stems decumbent to erect, 1-3.5 dm high, green to purplish tinged, terete, striate; leaves opposite or alternate, 2-7 cm long, 1-4 mm wide, linear to lanceolate, sessile, marginal glands up to 15 with 1 at acute apex; heads solitary at the ends of branches; peduncles 2.2-3.2 cm long; phyllaries 5, purple to green tinged, 8.9-11.1 mm long, 2.3-3.6 mm wide, linear-oblong, rounded on the back with 2 rows of linear glands, apex acute to truncate; flowers *ca.* 40, corolla 5.4-6.5 mm long, tube puberulent, greenish, longer than the purple funnelform throat; pappus 5.4-6.7 mm long, straw-colored, usually purple tinged, bristles hispidulous; achenes 5.5-6.5 mm long, hispidulous.

FLOWERING TIME: August through November.

TYPE: Mexico. *Bonpland 4188*, fragment (F!).

DISTRIBUTION: Jalisco and Queretaro through the Valley of Mexico to Oaxaca and Vera Cruz (Fig. 17). Collections from Durango are probably from populations introduced as roadside weeds.

This species and *P. coloratum* have often been considered conspecific (Robinson & Greenman, 1896; Rydberg, 1916). However, reference to the holotypes clearly shows that *P. coloratum* is a perennial whose involucral bracts are often green with purple dots, especially in the buds. In addition, heads of *P. coloratum* are not glaucous. *P. tagetoides* is more similar to *P.*

linaria than to *P. coloratum*. Certain specimens of *P. tagetoides* lack the glaucous distal ends of the phyllaries thereby resembling *P. linaria*. In addition to being perennial, *P. linaria* has phyllaries which are either completely, or not at all, glaucous. Therefore, first year, non-glaucous plants of *P. linaria* may be confused with *P. tagetoides*. In this case one may have to rely on collection locality as an aid in determining the correct species since the distributional ranges of these three species do not overlap.

Representative specimens: MEXICO. Durango. 47 mi w of Mapimi on the road to El Palmito, 18 Sep 1938, *Shreve 8792* (ARIZ, MICH, US). Jalisco. About 25 mi n w of Lagos de Morena, 2 Oct 1955, *Johnston 2869B* (SMU, TEX). Guanajuato. 20 mi n w of Irapuato, 28 Aug 1947, *Barkley, Rowell & Paxson 753* (MICH, TEX). Querétaro. 1910-1913, *Arsene 10536* (GH, US). Michoacan. Near Morelia, 19 Sep 1919, *Arsene 9007* (GH, MO, US). Mexico. Rio Hondo, 3 Nov 1895, *Pringle 6232* (F, GH, MICH, MO, ND, US). Hidalgo. Zimapán, 11 Aug 1948, *Moore & Wood 4459* (NY). Pueblo. Tehuacán, 20 Aug-8 Sep 1905, *Rose, Painter & Rose 9946* (US). Veracruz. 15 mi w of Orizaba, 18 Nov 1959, *Graham & Johnston 4779* (TEX). Morelos. Near Yautepec, 28 Oct 1902, *Pringle 8680* (GH, MO, UC, US). Oaxaca. Las Sedas, 8 Sep 1894, *Smith 265* (MO, NH, UC, US).

15. **Porophyllum linaria** (Cav.) DC., Prodr. 5:649. 1836.

Cacalia linaria Cav., Ic. 3:29. 1794.
Hunteria columbina Moc. & Sessé *ex* DC., Prodr. 5:649. 1836.
Porophyllum linarifolium St.-Lag., Ann. Soc. Bot. Lyon 7:203. 1880.

Perennial, suffruticose, glabrous, glaucous; stem 2.5-5 dm high, branching from near the base or above, green to purplish tinged, becoming brownish-purple with age, terete, striate to angled; leaves opposite or alternate, sessile, 2-4.5 cm long, narrowly linear, sometimes revolute, with 2 rows of oblong glands; heads corymbose; peduncles 0.9-2 cm long; phyllaries 5, purple, usually glaucous, 8-10.5 mm long, 2-4.2 mm wide, oblong with 2 rows of linear glands, apex widely acute; flowers *ca.* 35-40, corolla 5.1-5.8 mm long, purple, rarely white, puberulent, tube slightly longer than the funnelform throat; pappus 4.5-5.5 mm long, straw-colored, purple tinged, bristles hispidulous; achenes linear or longitudinally curved, 4.5-5.5 mm long, hispidulous.

Flowering time: August through November.

Type: Mexico. Querétaro, photo (!), Jardín Botánico, Madrid.

Distribution: Coahuila, San Luis Potosí and Aguascalientes (Fig. 17).

This species is quite similar to *P. tagetoides* and is discussed under that species. Although the ranges of the two species do not overlap at the present, *P. tagetoides* tends to be a weedy species and might be introduced into the range of *P. linaria*. *P. linaria* is also similar to *P. filiforme* (less so than to *P. tagetoides*) and the two are found growing side by side. The sheet listed from Aguascalientes (*Rose & Painter 7765*) has some heads with white flowers (GH).

Representative specimens: MEXICO. Coahuila. Carneros Pass, 9 Sep 1889, *Pringle 2397* (F, GH, MO, ND, NY, UC, US). San Luis Potosí. Minas de San Rafael, Nov 1910, *Purpus 4785* (F, GH, MO, UC, US). San Pedro, 11 Aug 1934, *Pennel 18071* (LL, MICH, NY, US). Aguascalientes. Near Aguascalientes, 9 Oct 1903, *Rose & Painter 7765* (GH, US).

16. **Porophyllum filiforme** Rydberg, N. Amer. Fl. 34:190. 1916.

Porophyllum filifolium Gray, Proc.fl Amer. Acad. 19:35. 1883, not *P. filifolium* DC., 1836.

Perennial herb with a slender woody caudex, glabrous; stems erect, branching from near base or above, 2.5-4 dm high, green to purple tinged, terete, striate; leaves alternate, sessile, 1-5 cm long, filiform with numerous glands, 1 at apex; heads solitary at the ends of branches; peduncles 0.5-4 cm long; phyllaries 5, purple, often with white to pale purple margins, 7-9 mm long, 8-5.7 mm wide, obovate, rounded on the back with 2 rows of linear glands, apex rounded to truncate; flowers *ca.* 35-40, corolla 4.1-5.5 mm long, straw-colored to purple, bristles hispidulous; achenes 4.5-5.5 mm long, hispidulous.

Flowering time: August through November.

Type: Coahuila. Sierra Madre south of Saltillo, 1880, *Palmer 688* (US!).

Distribution: Coahuila, Nuevo Leon, and San Luis Potosí (Fig. 17).

This species might be confused with *P. linaria* but can be distinguished by its short, wide phyllaries and filiform leaves. *Porophyllum filiforme* and *P. linaria* are sometimes found growing together.

Representative specimens: MEXICO. Coahula. Carneros Pass, 3 Sep 1889, *Pringle 2401* (F, MICH, MO, ND-G, UC, US). Nuevo Leon. 9 mi from Galeana on the road to Iturbide, 9 Oct 1959, *Graham & Johnston 4218* (TEX). Loma, 23 Aug 1940, *Shreve & Tinkham 9649* (ARIZ). San Luis Potosi. Minas de San Rafael, Nov 1910, *Purpus 4786* (UC).

17. **Porophyllum warnockii** R. R. Johnson, Brittonia 18:96. 1966.

Shrub, glabrous, sometimes glaucous, foliage and heads with scattered, minute whitish dots; stems erect, purplish-green when young becoming purple with age, terete, striate; leaves mostly alternate, some opposite, sessile, 2-6 cm long, filiform, with several large reddish-brown glands scattered along the leaf and one at the acute apex; heads solitary at the ends of branches or in open corymbs; peduncles *ca.* 1-2 cm long; phyllaries 5, green to purplish, 11.7-14.4 mm long, 1.7-2.1 mm wide, linear, with 1 to 2 rows of linear glands, apex sharply acute; flowers 20-25, corolla 6.8-8.4 mm long, hispidulous, pinkish-white, tube *ca.* twice as long as the narrowly funnelform throat; pappus 6-7.8 mm long, straw-colored, bristles hispidulous; achenes 6.3-7.9 mm long, scabrescent.

Flowering time: September through December.

Type: Mexico. State of Mexico, District Temascaltepec, Nanchititla, along cliffs, 20 Sep 1935, Hinton 8469 (GH!); isotypes (F! LL! MICH! UC!).

Distribution: Cliffs and dry slopes in the state of Mexico (Fig. 17).

This species shows greatest morphological resemblance to *P. coloratum* and *P. obtusifolium*. It differs from both these species by having longer phyllaries (phyllary length to width ratio of at least 6.6:1) and filiform leaves.

Porophyllum tagetoides, the only other species of *Hunteria* which occurs in the state of Mexico, is a small herbaceous plant with shorter, wider phyllaries than the suffrutescent *P. warnockii*. The long, strictly filiform leaves separate *P. warnockii* from all other species of the Mexican mainland except *P. filiforme*, which occurs in northern Mexico and differs by the characters given in the key to the species. In addition, *P. warnockii* differs from all other species of *Porophyllum* by the minute, scattered, whitish dots, the most obvious character for identification of the species. (This species was named after Barton H. Warnock, Sul Ross State College, authority on the flora of the Trans-Pecos region of Texas.)

The only collection known, in addition to the type collection, is the following: State of Mexico. Tonatico, in a forest clearing on a dry hillside, 1550 m, 14 Dec 1952, *Matuda et al. 27521* (NY).

18. **Porophyllum coloratum** (HBK) DC., Prodr. 5:650. 1836

Kleinia colorata HBK, Nov. Gen. & Sp. 4:158. 1820.
Porophyllum seemanii Schultz-Bip. *in* Seem., Bot. Voy. Herald: 308. 1857.
Porophyllum simplex M.E. Jones, Contr. West. Bot. 12:46. 1908.

Perennial, glabrous; stems erect, slender, branching above, 4 dm or more high, green to purple tinged, becoming brown with age, terete, striate; leaves opposite or alternate, subsessile to short petioled, 1-5 cm long, 2-8 mm wide, linear to lanceolate or oblanceolate, marginal glands up to 9 with 1 at the acute to obtuse apex; heads solitary at the ends of branches or in clusters of 2 or 3; peduncles 1-4 cm long; phyllaries 5, purplish, often with green base bearing purple dots, 8-10.5 mm long, 1.8-2.5 mm wide, linear to linear-oblong, rounded on the back with 2 rows of linear glands, apex acute to acuminate; flowers *ca.* 30-35, corolla 5.8-6.4 mm long, purple, or tube yellowish, longer than the purple funnelform throat; pappus 5-6 mm long, straw-colored, often tinged with purple, bristles hispidulous; achenes 5-5.9 mm long, hispidulous.

Flowering time: September to February.

Type: Mexico. Guanajuato. Photograph (US!).

Distribution: Southern Sonora and Chihuahua, south through Jalisco (Fig. 17).

Although this species has been confused with *P. tagetoides*, the two are quite distinct (see discussion under that species).

Representative specimens: MEXICO. Sonora. Dist. Alamos, Saucito Canyon, 11 Oct 1933, *Gentry 479 M* (US). N w base of Cerro Colorado, 10 Dec 1939, *Gentry 5209* (ARIZ, F, MICH, MO, NY, UC, US). Chihuahua. Guasaremos, Rio Mayo, 29 Sept 1936, *Gentry 2904* (ARIZ, F, GH, MO, UC, US). Batopillas, 8 Oct 1898, *Goldman 257* (NY). Sinaloa. Cacalatan, Picacho, Sep 1932, *Ortega 7154* (F, US). Durango. Sierra Gamon, Canyon Cantero, 21 Sep 1948, *Gentry 8386* (MICH, UC). Nayarit. Tepic, 5 Jan-6 Feb 1892, *Palmer 1901* (ARIZ, F, MICH, NY, UC, US). Jalisco. Guadalajara, 31 Oct 1889, *Pringle 2446* (MICH, MO, UC, US) in part.

19. **Porophyllum obtusifolium** DC., Prodr. 5:650. 1836.

Perennial, suffruticose, glabrous; stems erect, slender, branching above, 4 dm or more high, green to purple tinged, terete, striate; leaves opposite or alternate, sub-sessile, 1-4 cm long, 2-11 mm wide, variable, oblong, oblanceolate or lanceolate, glands up to 9 with 1 at the acute to widely obtuse apex; heads solitary at the ends of branches or in a terminal, often crowded, racemose or corymbose inflorescence; peduncles 0.4-2.9 cm long; phyllaries 5, purplish, often with green base bearing purple dots, 7.8-10.5 mm long, 2-3 mm wide, linear to linear-oblong, rounded on the back with 2 rows of linear glands, apex acute to acuminate; flowers *ca.* 30-35, corolla 4.9-6.7 mm long, dirty white to very pale purple or red, tube longer than the funnelform throat; pappus 4.9-6 mm long, straw-colored to purple tinged, bristles hispidulous; achenes 4-6.3 mm long.

FLOWERING TIME: August through February.

TYPE: Mexico (near Villalpando, *fide* Rydberg, 1916), 1829, *Mendez*; photograph (US!).

DISTRIBUTION: Jalisco, Guanajuato, and Michoacán (Fig. 17).

Porophyllum obtusifolium appears very similar to *P. coloratum* but has pale corollas. In one collection from Guadalajara (*Pringle 2446*) both species were mounted on the same sheet (UC). This is the only area in which the two species have been collected together.

REPRESENTATIVE SPECIMENS: MEXICO. JALISCO. Guadalajara, 31 Oct 1889, *Pringle 2446* F, ND, NY, SMU, UC) in part. Bolanos, 15-17 Sep 1897, *Rose 2948* (US). GUANAJUATO. Montagues, Aug 1897, *Duges 479* (GH). MICHOACAN. Near Morelia, 5 Feb. 1912, *Arsene 9931* (US).

20. **Porophyllum amplexicaule** Engelm., **ex** Gray, Pl. Wright. 1:120. 1852.

Perennial, glabrous, usually glaucous, fruticose at base; stem erect, up to *ca.* 5 dm high, green, becoming brown with age, terete, striate; leaves mostly opposite, alternate on upper branches, 1.4-3 cm long, 2.5-7.5 mm wide, lanceolate, semi-amplexicaul, entire, acute, slightly fleshy with several small dark sub-marginal glands; heads solitary at the ends of branches; peduncles 4-6 cm long, thickened below the involucre; phyllaries 8-10, green, 10.8-13.2 mm long, 2.8-4.1 mm wide, broadly linear, bluntly acuminate; glands linear, in 4 or more irregular rows; flowers 80 or more, corolla 6.4-7 mm long, narrow, cylindric throat and tube approximately equal length; pappus 5.8-7.2, dark straw-colored, bristles scabrous; achenes 5-6.3 mm long, hispidulous.

FLOWERING TIME: June through November depending on rainfall and temperature.

TYPE: Mexico. Coahuila. Near Mesillas, 1848-49, *Gregg 524* (NY!); isotype (GH!).

DISTRIBUTION: Southeastern Coahuila (Fig. 18).

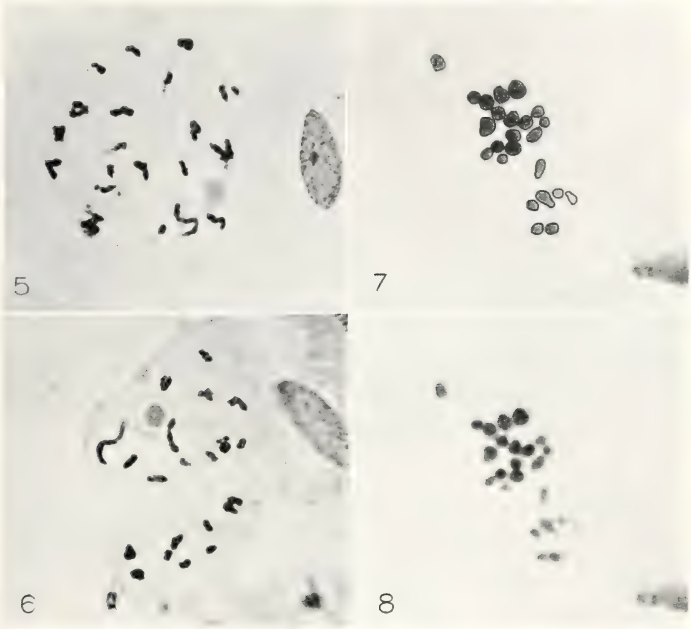

FIG. 5. Diakinesis in a microsporocyte from *P.* x *fruticulosum*, a natural hybrid between *P. amplexicaule* and *P. scoparium* (× 5375).

FIG. 6. Diakinesis in another microsporocyte from *P.* x *fruticulosum* showing univalents, bivalents and multivalents (× 4630).

FIG. 7. Retouched photograph of metaphase I in a microsporocyte of an F_1 hybrid (*P. scoparium* x *P. gracile*) with the 12 univalents and 12 bivalents outlined (× 7080).

FIG. 8. Photograph of the cell shown in Fig. 7 (× 7080).

This comparatively rare species has a restricted distribution. In addition, many of the plants collected and identified as *P. amplexicaule* are probably resultant progeny of hybridization between *P. amplexicaule* and *P. scoparium* followed by backcrossing to *P. amplexicaule*. *P. amplexicaule* has been reported to have a gametic number of 12 chromosomes (Turner, et al., 1961). Specimens which appear to be "pure" *P. amplexicaule*, recently collected in Coahuila, and their greenhouse progeny show meiotic configurations of varying numbers of univalents, bivalents, and multivalents (Fig. 4) and pollen fertility of less than 50 %. These meiotic cells are similar

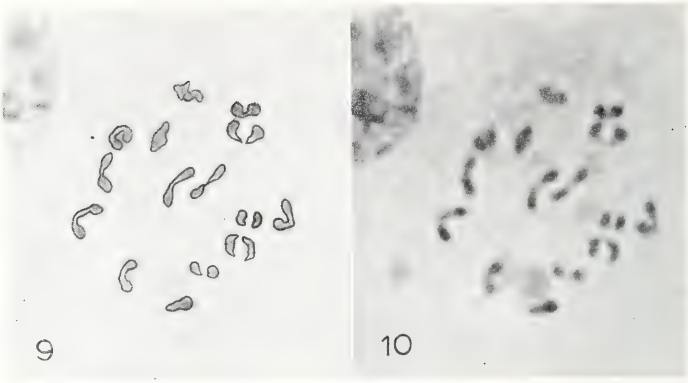

FIG. 9. Retouched photograph of diakinesis in a microsporocyte of *P. tridentatum* var. *crassifolium* with the 15 bivalents outlined (× 7275).

FIG. 10. Photograph of the cell shown in Fig. 9 (× 7275).

to those observed in *P. fruticulosum* Rydb., apparently a natural hybrid between *P. amplexicaule* and *P. scoparium* (see discussion under *P. scoparium*).

REPRESENTATIVE SPECIMENS: MEXICO. COAHUILA. 11.1 mi n of Saltillo, 24 Jul 1959, *Rock M251* (TEX). 19.3 mi w of Saltillo, 13 Nov 1963, *Johnson 2360* (KANU). Ramos Arizpe, 14 Jun 1936, *Wynd & Mueller 25* (ARIZ, GH, MO, ND, NY).

21. **Porophyllum scoparium** Gray, Pl. Wright. 1:119. 1852.

Perennial, suffruticose, glabrous; stems much branched, 2-6 or more dm high, erect, green, becoming brownish with age, terete, scarcely striate; leaves sessile, opposite in seedlings, mostly alternate in mature plants, sessile, filiform, somewhat fleshy, up to 4 cm long, with numerous small dark glands, apex acute to acuminate; heads solitary at the ends of branches; peduncles 1-2 cm long or shorter, greatly enlarged at base of involucre; phyllaries 7-9, green to yellowish, 6-9.3 mm long, 1.5-2.3 mm wide, linear to oblanceolate, usually with 2 rows of long, linear glands on the rounded back, apex acute; flowers more than 45, corolla 5.3-8 mm long, yellow, tube shorter than the cylindric throat; pappus 5.4-7.5 mm long, yellowish, bristles hispidulous; achenes 3.7-5.5 mm long, hispidulous.

FLOWERING TIME: Throughout year, depending on rain and temperature.

TYPE: Texas. West Texas to El Paso, May-Oct 1849, *Wright 369* (US!); rocky banks of the San Pedro River, and mountains east of El Paso (*fide* Gray, 1852); isotypes (GH! NY! UC!).

DISTRIBUTION: Southern New Mexico, southwestern Texas, Chihuahua,

Coahuila and Nuevo León (Fig. 18). It may occur elsewhere as an introduced weed, especially along roadsides.

This species and *P. amplexicaule* are morphologically similar. *P. amplexicaule* has a very restricted distribution, its range being entirely encompassed by that of *P. scoparium*. Both species are commonly found on limestone, as are several other species of the genus. *P. fruticulosum* Rydb. is apparently a hybrid between *P. scoparium* and *P. amplexicaule* and should thus be designated *Porophyllum* X *fruticulosum* (*P. amplexicaule* X *P. scoparium*) to conform to the International Code of Botanical Nomenclature. Meiotic configurations from plants fitting the description of *P.* X *fruticulosum*, collected in Coahuila, show various numbers of univalents, bivalents and multivalents (Figs. 5, 6). In addition, heads from several plants of *P.* X *fruticulosum* grown in the greenhouse produced either no pollen or pollen of low fertility. Although *P. amplexicaule* and *P. scoparium* may have been ecologically or geographically separated at one time they now both occur along roadsides with *P.* X *fruticulosum*. *Porophyllum scoparium* is one of the more common roadside weeds throughout much of its range.

Porophyllum scoparium and *P. gracile* may be the ancestors of the now rare *P. greggii*. The gametic chromosome number for *P. scoparium* is 12 (Jackson, 1960; Powell & Turner, 1963; Table 1, Fig. 3).

Representative specimens: UNITED STATES. New Mexico. Otero Co., Sacramento Mts., Dog Canyon, 5 Apr 1962, *Johnson 1502* (KANU). Dona Ana Co., Organ Mts., 21 Oct 1906, *Wooton & Standley (US 564236)*. Texas. El Paso Co., El Paso, *Whitehouse 286* (MO, NY, SMU, UC). Culberson Co., 6½ mi n w of Van Horn, *Waterfall 5456* (GH, MO, NY). Brewster Co., Chisos Mts., Blue Creek, 38 Jun 1931, *Mueller 8240* (F, GH, MICH, MO, NY, TEX, UC, US). Val Verde Co., west wall of Pecos River Canyon, 21 Jun 1941, *Innes, Moon & Warnock 1290* (GH).

MEXICO. Chihuahua. Ciudad Juarez, 26 Sep 1902, *Pringle 9953* (F, MO, NY, UC, US). Coahuila. Jimulco Mts., 22 Apr 1885, *Pringle 207* (F, GH, MICH, NY, UC, US). 30 mi s w of Monterrey, 1 Dec 1945, *Warnock & Barkley 14810M* (GH, MO, NY, TEX, UC). Nuevo Leon. 23 mi n e of Monterrey, 14 Nov 1963, *Johnson 2378* (KANU).

22. **Porophyllum greggii** Gray, Pl. Wright. 1:120. 1852.

Perennial, glabrous herb; stems green, 1.5-3 dm high, flexuous, weak, semierect, terete, striate; leaves alternate, sessile, up to 6 cm long, filiform with many small glands; heads solitary at the ends of branches; peduncles 2-4 cm long; phyllaries 5, light green, scarious-margined, 8.9-12 mm long, 3.4-5.5 mm wide, elliptical to obovate-oblong with 2 rows of linear or oblong, yellowish glands, apex rounded; flowers more than 50, corolla yellow, 7.6-9.8 mm long, tube slightly shorter than the cylindric throat; pappus 8-9 mm long, straw-colored, bristles hispidulous; achenes 6.8-8 mm long, densely puberulous with tawny hairs.

Flowering time: May through October, depending on rain.

Type: Texas. West Texas to El Paso, May-Oct 1849, *Wright 370* (GH!); isotype (UC!). From hills in the Pass of the Limpia (*fide* Gray, 1852).

DISTRIBUTION: Big Bend, Trans-Pecos region of west Texas (Fig. 18).

Although Gray (1852) considered plants from the Valley of Parras, Coahuila, as this species, the specimens from that area are actually *P. scoparium* or hybrids between *P. amplexicaule* and *P. scoparium*, called *P. fruticulosum* by Rydberg (1916). Although specimens from the collection of the Mexican Boundary Survey and into the early 1900's are not common, they are more numerous than recent collections. Barton H. Warnock, Sul Ross State College (personal communication), informs me that the species is now rare. It is reportedly browsed and has apparently suffered from overgrazing.

Porophyllum greggii has involucral characteristics similar to *P. gracile*, flower characteristics like *P. scoparium*, and the foliage is intermediate between the two. Certain of the *P. scoparium* X *P. gracile* F_1 hybrids grown during this study resembled *P. greggii*. Since the ranges of *P. scoparium* and *P. gracile*, reportedly, formerly overlapped in southwestern Texas (Coulter, 1892; Gould, 1962) it is highly probable that *P. greggii* developed from hybridization between those two species.

REPRESENTATIVE SPECIMENS: TEXAS. Jeff Davis Co., Davis Mts., ca. Fenley Rch., 17 Oct 1936, *Hinckley 877* (F, LL, NY, SMU, UC). Brewster Co., Glass Mts., Altuda Pt., 6 Jun 1941, *Warnock* (GH, TEX). Presidio Co., San Estaban Canyon, 28 May 1957, *Warnock & McBryde 14539* (SRSC).

23. **Porophyllum gracile** Benth., Bot. Voy. Sulph. 29. 1844.

Porophyllum junciforme Greene, Leaflets Bot. Obs. 2:154. 1911.
Porophyllum vaseyi Greene, Leaflets Bot. Obs. 2:154. 1911.
Porophyllum caesium Greene, Leaflets Bot. Obs. 2:155. 1911; not *P. caesium* Casar., 1845.
Porophyllum leucospermum Greene, Leaflets Bot. Obs. 2:155. 1911.
Porophyllum confertum Greene, Leaflets Bot. Obs. 2:155. 1911.
Porophyllum ochroleucum Rydb., N. Amer. Fl. 34:189. 1916.
Porophyllum cedrense Rydb., N. Amer. Fl. 34:189. 1916.
Porophyllum pinifolium Rydb., N. Amer. Fl. 34:192. 1916.
Porophyllum confertum var. *ochroleucum* I. M. Johnston, Proc. Calif. Acad. IV, 12:1209. 1924.
Porophyllum putidum A. Nels., Amer. Jour. Bot. 18:440. 1931.
Porophyllum nodosum M E. Jones, Contr. W. Bot. 18:82. 1933.

Perennial, suffrutescent, glabrous, often glaucous; stems little to much branched, 2-6 dm high, sub-erect to erect, green to purplish becoming brownish to purplish with age, terete, striate; leaves opposite in seedlings, mostly alternate in mature plants, sessile, filiform to linear, up to 5 cm long, usually less than 2 mm but up to 5 mm wide, apex acute to obtuse; heads solitary at the ends of branches; peduncles 0.4-2.5 cm long, moderately enlarged at base of involucre; phyllaries 5, green to purple, 9.3-14.6 mm long, 1.4-3.5 mm wide, linear to oblong, apex obtuse, seldom acute, rounded on the back with round to linear glands in 2 rows, rarely scattered; flowers 12-30, rarely as few as 5, corolla 6-9.1 mm long, white to pale purple with dark purple streaks, tube shorter to longer than the funnelform throat; pappus

5.3-8.6 mm long, white to purplish, bristles hispidulous; achenes 5.7-10.3 mm long, hispidulous.

Flowering time: Throughout year, depending on rain and temperature.

Type: Mexico. Baja California. Bay of Magdalena; not seen (Bentham *in* Hinds, 1844).

Distribution: Extreme southeastern Nevada through southern California, Arizona, and Baja California; also scattered collections from western Sonora, southern New Mexico and western Texas (Fig. 18).

This is one of the most variable species of the genus. *Porophyllum gracile* occupies the widest range of ecological habitats for a member of the section *Hunteria* and probably for the genus. In addition *P. gracile* occurs in not only the driest areas (rainfall of less than five inches a year) but also the coldest areas occupied by a species of *Porophyllum*. *P. gracile* is the only entirely polyploid (n=24) species known for the genus (Table 1). *Porophyllum ruderale*, another species with an extremely large and variable range, may have both diploid and polyploid races. Raven and Kyhos (1961) reported a gametic number of 22 ($2n$=44) for the species (subsp. *ruderale*?) while Diers (1961) reported a $2n$ number of 22.

The occupation of a large geographic area and, in many cases, extreme environmental conditions by polyploids because of a wide range of tolerances was suggested by Diers (1961) and was also discussed by Stebbins (1950).

I consider the plants formerly called *P. confertum* and *P. ochroleucum* as *P. gracile*. Johnston (1924) discussed perplexing intermediate specimens, also examined during this study, and predicted that future collecting would probably show the three to be conspecific. Separation of the *P. gracile* complex strictly on a morphological basis, in the past, resulted in the naming of nearly a dozen species. The populations from almost every island off the coast of Baja California are detectably different. This has resulted in naming of *P. cedrense* (Rydberg, 1916) as well as *P. confertum* (Greene, 1911). Hybridization experiments with plants morphologically and geographically assignable to *P. gracile*, *P. junciforme*, *P. caesium*, *P. leucospermum*, and *P. putidum* have resulted in the production of offspring with high pollen fertility which show no irregularities during meiosis.

Coulter (1892) listed *P. gracile* as occurring on "arid plains of southwestern Texas." Specimens in the Mexican Boundary Survey collection indicate that the species may have formerly been more common along the Rio Grande Valley and the adjacent region. Unfortunately the information with these collections is scanty. The only place that *P. gracile* is known to grow in Texas today is in the Franklin Mountains of El Paso County.

Porophyllum gracile and *P. scoparium* are allopatric except for plants in the Franklin Mountains. Since both species were formerly in southwestern Texas and both are commonly found growing on limestone in the Lower

Sonoran Life Zone, it is highly probable that the now rare *P. greggii* arose from hybridization and subsequent backcrossing between these two species.

In the spring of 1962, *P. gracile* achenes collected in the field (RRJ 61-122) were planted in the greenhouse with transplants of *P. scoparium* (RRJ 1502). Attempted crosses between these resulted in fertile achenes when *P. scoparium* was used as the pistilate parent. However, only infertile achenes were produced if *P. gracile* was used as the pistilate parent. During the course of this study various collections of *P. scoparium* and *P. gracile* from throughout their ranges were repeatedly crossed but no viable seed was obtained using *P. gracile* as the pistilate parent.

Considerable difficulty was encountered in culturing the F_1 triploids. Although seeds sprouted quite readily in Petri dishes partially filled with water, or on moist filter paper, the resulting seedlings usually died within one week to three months. By the summer of 1963 ten hybrids from two different *P. scoparium* X *P. gracile* crosses had grown past the seedling stage. Eight of these matured and flowered. Two, although apparently vegetatively mature, never flowered. One of those two died within a year, appearing much like an annual. The other is still alive and obviously a perennial, after about a year and a half of continuous vegetative growth.

TABLE 2. Pollen Size and Stainability in Greenhouse Plants.

Species	Percent Stainable	Average Size in Microns	Locality of Seed Source
P. gracile	91.3	34.79	NEVADA, Clark Co., Searchlight, RRJ 1871
	98.7	35.42	ARIZONA, Yavapai Co., 12 mi. S. of Cordes Jctn., RRJ 61-122
	98.2	37.68	SONORA, Cholla Bay, Rocky Point, RRJ 1818
P. scoparium	98.8	33.58	NEW MEXICO, Otero Co., Sacramento Mts., Dog Canyon, RRJ 1502
	98.2	32.90	TEXAS, El Paso Co., El Paso, RRJ 1547
F_1 Hybrids (*P. scoparium* × *P. gracile*)	4.0-13.6*	21.25-66.61**	
P. tridentatum var. *crassifolium*	99.9	31.10	BAJA CALIFORNIA, San Bruno Island, Carter & Reese 4538

* Averages for the two extreme plants.
** Extremes for pollen size from all plants.

Pollen fertility of *P. gracile*, *P. scoparium*, and their hybrids was determined by staining with cotton blue in lactophenol and propionic acid. The pollen produced by the hybrids was extremely variable in size (21.25-66.61 microns) in contrast to 31.19-35.42 for *P. scoparium* and 33.67-40.85 for *P.*

gracile. In the hybrids, pollen stained at varying intensities but only grains which stained a uniform deep blue, usually greater than 35 microns in diameter, were considered fertile. Pollen size and fertility of *P. gracile* and *P. scoparium* from different localities is compared with the hybrids in Table 2. In addition to low fertility, mechanical failure of the anthers often, and in one hybrid consistently, resulted in little, if any, pollen dispersal.

The F_1 hybrids, with strictly filiform leaves, were vegetatively nearer to *P. scoparium* than *P. gracile* but did not produce the characteristic woody base of *P. scoparium*. However, they were somewhat nearer to *P. gracile* in head characters. They all had involucres with five phyllaries and long gracile shaped achenes. Although the corollas were shaped like those of *P. gracile* and bore dark streaks like *P. gracile*, they showed some yellow color of *P. scoparium*. In general appearance the species *P. greggii* is very similar to some of these hybrids.

Except in one flower, meiotic stages of *P. gracile* grown from 11 localities were regular. A bridge and fragment in this one flower was probably due to a spontaneously developed abnormality such as an inversion. All other material showed normal meiosis with formation of 24 pairs during diakinesis and metaphase I.

Samples of *P. scoparium* from six localities throughout its range showed no irregular meiosis. Crosses between plants from three of these localities produced fertile offspring which formed 12 pairs of chromosomes, like their parents, and underwent normal meiosis.

In more than 100 pollen mother cells examined from the F_1 hybrids, in all stages from anaphase I through telophase II, no irregularities such as bridges and fragments or excluded chromosomes were found. Occasional lagging chromosomes were noted.

Attempted crosses between 38 heads of eight hybrids failed. In 65 backcrosses to either *P. gracile* or *P. scoparium*, no fertile achenes were obtained. In addition, 42 heads hand pollinated with pollen of both parents remained sterile. Further, several hundred heads in close proximity to both parental species (each of which open pollinates naturally, and regularly produces fertile achenes in the greenhouse) were checked without securing a single fertile F_1 achene.

Examination of 63 microsporocytes from the *P. scoparium* X *P. gracile* hybrids showed 24 chromosomal configurations during diakinesis and metaphase I (Figs. 7, 8). Due to the small size of the chromosomes of *Porophyllum*, it was not always possible to determine which of these configurations were bivalents and which were univalents. Since none was a multivalent, to derive 24 configurations from 36 chromosomes (24 from *P. gracile* and 12 from *P. scoparium*) the only combination possible would be 12 bivalents and 12 univalents. Further, since nothing but bivalent formation was

observed in *P. gracile* one might postulate that *P. gracile* is an allotetraploid, probably of two diploid species (Stebbins, 1950). Therefore, the 12 bivalents in the hybrid would be formed by the 12 *P. scoparium* chromosomes pairing with 12 homologous *P. gracile* chromosomes (originally derived from a *P. scoparium* genome), while the 12 univalents represent another genome, derived from the unknown ancestor of *P. gracile*.

On the other hand, *P. gracile* might be a segmental allotetraploid with a genomic constitution of A_1 A_1 A_2 A_2. Thus, autosyndetic pairing would occur between the two sets of chromosomes from *P. gracile* while the 12 unpaired chromosomes would be those from *P. scoparium*. A similar case was found in *Haplopappus spinulosus* subsp. *australis* (n=8) when crossed with *Haplopappus gracilis*. Four bivalents were often formed by the eight *H. s. australis* chromosomes during meiosis in the F_1 hybrids (Jackson, 1962).

Representative specimens: UNITED STATES. Nevada. Clark Co., 4 mi n of Logandale, 23 Oct. 1963, *Johnson 2120* (KANU). California. San Bernardino Co., Tecopa Pass, Kingston Range, 10 Jun 1951, *Alexander & Kellog 2336* (UC). Riverside Co., 2 mi from Cottonwood Springs, Cottonwood Mts., 15 May 1938, *Ferris & Rosshach 9537* (F, GH, MICH, UC). San Diego Co., El Cajon, 29 May 1894, *Brandegee* (UC). Imperial Co., 14 mi e of Beale's Well, Chocolate Mts., 26 Mar 1941, *Wiggins 9653* (GH, MO, UC). Arizona. Coconino Co., Havasupai Canyon, 4 Sep 1943, *Clover 7053* (LL, MICH). Gila Co., Roosevelt Lake, 12 Aug 1962, *Johnson 1707* (KANU, TONTO NAT'L MON.). Pima Co., foothills of Santa Catalina Mts., Apr 1881, *Pringle 13750* (F, GH, MICH, MO). Cochise Co., Whetstone Mts., May-Oct 1903, *Purpus* (UC, US). New Mexico. Grant Co., Upper Corner Monument, 3 May 1892, *Mearns 150* (US). Hidalgo Co., Apache Hills, 11 May 1957, *Jackson 2368* (UNM). Texas. El Paso Co., Franklin Mts., 25 Oct 1958, *Warnock & Johnston 17042* (SRSC).

MEXICO. Baja California. 20 mi s of Tia Juana, 3 Apr 1931, *Wiggins 5121* (ARIZ, LL, MICH, MO, UC, US). Angel de la Guarda Is., 23 Mar 1959, *Moran 7193* (F, UC). Cedros Is., 1 Apr 1897, *Brandegee* (UC). Magdelena Is., 12 Jan 1889, *Brandegee* (F, GH, UC). Santa Catalina Is., 14 Apr 1952, *Moran 3875* (UC). Cape San Lucas, 30 Dec 1905, *Nelson & Goldman 7377* (GH, US). Sonora. Cholla Bay, Rocky Point, 27 Feb 1958, *Raven 11669* (UC). San Bernardo, Rio Mayo, 12 Feb 1935, *Gentry 1299* (ARIZ, MO, UC).

24. **Porophyllum maritimum** Brandg., Zoe 5:162. 1903.

Perennial, fruticose, glabrous to tightly tomentose, glaucous; stem *ca.* 2 dm high, green, becoming reddish-brown with age, divaricately branched from the base, terete, striate; leaves mostly opposite, sessile, up to 3 cm long, 1-4 mm wide, terete, fleshy, acuminate with several oblong glands, 1 at the apex; heads solitary at the ends of branches or in upper leaf axils; peduncles 0.5-4 cm long; phyllaries 5, green to purple or reddish tinged, glaucous, 10.5-13.3 mm long, 2.5-3.1 mm wide, oblong, obtuse to acute with 2 rows of linear or oblong glands; flowers 20-40 or more, corolla pale, 6-7 mm long, tube nearly equal to funnelform throat; pappus 6-8 mm long, straw colored to reddish tinged, bristles hispidulous; achenes 7.5-8.6 mm long, hispidulous.

Flowering time: November through April and, according to Shreve and Wiggins (1964), after summer rains.

Type: Mexico. Baja California. Coast between San Jose del Cabo and Cabo San Lucas, Nov 1902, *Brandegee* (UC!); isotype (US!).

Distribution: Southern cape of Baja California (Fig. 19).

None of the specimens of *P. maritimum* examined was as glaucous as the type. Except for this species' mostly opposite, fleshy leaves, it is similar to *P. gracile*. It also differs from most specimens of *P. gracile* in the divaricate branching habit. *Porophyllum porfyreum* has strictly filiform, non-fleshy leaves, longer in relation to width than either those of *P. gracile* or *P. maritimum*. In addition the corolla of *P. porfyreum* is purple with lobes slightly tinged with orange (unique for the genus). *P. porfyreum* and *P. maritimum* are sympatric and *P. gracile* also occurs in the same area.

Representative specimens: Baja California. San Jose del Cabo, Mar-Apr 1899, *Grabendorfer* (UC). San Jose del Cabo, 17 Mar 1892, *Brandegee 331* (GH, UC).

25. **Porophyllum porfyreum** Rose & Standl. **in** Rydb., N. Amer. Fl. 34:191. 1916.

Slender shrub, glabrous, glaucous; stem green, becoming reddish brown with age, profusely branched, terete, striate; leaves opposite or alternate, sessile, narrowly linear to filiform, up to 5.5 cm long, glands few; heads solitary at the ends of branches; peduncles 1.5-4 cm long, thickened below base of involucre; phyllaries 5, purplish, glaucous, 9.3-13.2 mm long, 2.5-4.7 mm wide, oblong, obtuse to acute with small, scattered oblong to linear glands; flowers more than 40, corolla purple, slightly tinged with orange on lobes, 5.9-6.8 mm long, hispidulous, tube nearly equal to slightly longer than the funnelform throat; pappus 5.2-6 mm long, straw colored to purple tinged, bristles hispidulous; achenes 7.3-8.7 mm long, hispidulous.

Flowering time: December through March.

Type: Mexico. Baja California. San Jose del Cabo, 26 Mar 1911, *Rose 16478* (US!); isotype (NY!).

Distribution: Baja California, vicinity of San Jose del Cabo (Fig. 19). See discussion under *Porophyllum maritimum*.

Representative specimens: Baja California. San Jose Del Cabo, 17 Feb 1940, *Dawson 1166* (MICH). 12.2 km s w of San Jose del Cabo, 16 Dec 1947, *Carter, Alexander & Kellogg 2215* (UC, US).

26. **Porophyllum brachypodum** Robins., Proc. Amer. Acad. 35:341. 1900.

Glabrous shrub; stems branching above, glaucous, green, becoming reddish-brown with age, terete, striate; leaves alternate, sessile to short-petioled, blade 3-4 cm long, 2-8.5 mm wide, widely lanceolate to linear, apex acute, base cuneate, marginal glands large, oblong; heads in dense corymbs; peduncles 3-9 mm long; phyllaries 5, pale green, 10.3-11.5 mm long, 3.8-4 mm wide, oblong, with 2 rows of linear glands, apex obtuse; flowers *ca.* 25, corolla

7.5-8 mm long, cream with dark lines along the funnelform throat, tube puberulent, longer than the throat; pappus 6.2-6.5 mm long, straw-colored, bristles scabrous; achenes 7.6-8.2 mm long, hispidulous.

Flowering time: June.

Type: Mexico, Sonora. Guaymas, 5-11 June 1897, *Rose 1272* (US!).

Distribution: Known only from the type collection (Fig. 18).

This species is morphologically close to *P. pausodynum* and the two species occur in the same area. However, a series of specimens of *P. pausodynum* show no intergradation toward *P. brachypodum* in shape and width of lower leaves. In addition, the leaves of *P. pausodynum* are never petiolate. The inflorescence of *P. brachypodum* is a corymb in contrast to the cymes borne by *P. pausodynum*.

27. **Porophyllum pausodynum** Robins. & Greenm., Proc. Amer. Acad. 32:32. 1896.

Porophyllum seemanni S. Wats., Proc. Amer. Acad. 24:57. 1889; not *P. seemannii* Schultz-Bip, 1857.

Shrub; stems branching above, slightly glaucous, green, becoming reddish-brown with age, terete, striate to angled; leaves alternate or opposite, subsessile, 3-5 cm long, 2-5.5 mm wide, linear-oblanceolate to linear, glands large, oblong, marginal or submarginal, up to 9 with 1 at the acute to obtuse apex; heads in dense cymes; peduncles 0.7-1.2 cm long; phyllaries 5, pale green, 9.9-13.4 mm long, 2.6-5 mm wide, oblong with 2 rows of linear glands, apex obtuse; flowers *ca.* 25, corolla 6.9-7.6 mm long, cream with dark lines along the funnelform throat, tube puberulent, longer than the throat; pappus 6.9-9.8 mm long, straw-colored, bristles hispidulous; achenes 6.9-7.9 mm long, hispidulous.

Flowering time: March and April; October through December.

Type: Mexico. Sonora. Guaymas, 1887, *Palmer 279* (GH!); isotype (ND-G! NY! UC! US!).

Distribution: Guaymas and vicinity (Fig. 18). See discussion under *P. brachypodum*.

Representative specimens: Sonora. Guaymas, 24 Oct 1939, *Gentry 4737* (ARIZ, F, GH, MICH, MO, NY, UC, US). Guaymas, 23 Apr 1910, *Rose, Standley & Russel 15024* (GH, US).

28a. **Porophyllum tridentatum** Benth. var. **tridentatum**

Porophyllum tridentatum Benth., Bot. Voy Sulph. 30. 1844.

Low subshrub, up to 1 dm high; stem profusely branched, often decumbent, green, becoming reddish-brown to light brown or greyish with age, terete; leaves crowded on the stems, sessile, gland tipped, fleshy, cuneate, 0.5-1.2 cm long, apex 3-cleft with one gland at the end of each lobe; heads

solitary at the ends of branches; peduncle with minute, gland tipped hairs, *ca.* 0.5 cm long; phyllaries 5, green to purple tinged, scarious-margined, 7-9.9 mm long, 2.4-3.8 mm wide, oval, rounded on the back with 1 to several round to elliptical glands near the obtuse to rounded apex; flowers 25 to 40 or more, corolla yellowish, 5-5.9 mm long, tube shorter than the cylindro-funnelform throat; pappus straw-colored, 5.1-6.3 mm long, bristles hispidulous; achenes 2.8-3.2 mm long sparsely scabrescent to hispidulous.

Flowering time: November through May.

Type: Mexico. Baja California. Bay of Magdalena (Bentham *in* Hinds, 1844); not seen.

Distribution: Lower western side of Baja California in the vicinity of Magdalena Bay and adjacent islands (Fig. 19). See discussion under *P. tridentatum* var. *crassifolium*.

Representative specimens: Baja California. Magdalena Bay, 12 Jan 1889, *Brandegee* (NY, UC, US). Magdalena Island, 21 Jan 1889, *Brandegee* (F, US). Santa Maria Bay, 18 Mar 1911, *Rose 16264* (NY, US).

28b. **Porophyllum tridentatum** Benth. var. **crassifolium** (S. Wats.) I. M. Johnston, Proc. Calif. Acad. Ser. 4, 12:1211. 1924.

Porophyllum crassifolium S. Wats., Proc. Amer. Acad. 24:57. 1889.
Porophyllum leptophyllum I. M. Johnston Proc. Calif. Acad. Ser. 4, 12:1210. 1924.

Up to 3 dm high; leaves sessile, linear, up to 2.3 cm long, 3 mm wide, acute with one gland at the tip; phyllaries 6-7.8 mm long, 2.8-4 mm wide; achenes sparsely hispidulous to glabrate.

Flowering time: November through May.

Type: Mexico. Baja California. Muleje, 1887, *Palmer 423* (NY!); isotypes (NY! ND-G! UC! US!!).

Distribution: Eastern coast of central Baja California and islands in the Gulf of California (Fig. 19).

P. crassifolium and *P. tridentatum* are still considered separate species by some authorities (Shreve and Wiggins, 1964) even though Johnston, as early as 1924, stated that when the two are compared "relations are so obvious that a mere unit leaf-difference does not seem sufficient reason for keeping them distinct." I also found this to be the only consistent difference between the taxa and must agree with Johnston.

On the other hand, Johnston (1924) named a new species (*P. leptophyllum*) to the north of *P. tridentatum* var. *crassifolium* which supposedly had smaller leaves, smaller heads, and fewer flowers than *P. tridentatum* var. *crassifolium*. However, some specimens that I examined (from Tiburon Island), called *P. leptophyllum* by Johnston, had the small leaves that he ascribed to *P. leptophyllum* with the large heads typical of *P. tridentatum* var. *crassifolium* (*sensu* Johnston) and 30 to 40 flowers, rather than 25 to 30

flowers, as Johnston had reported. Thus, criteria that he used for the differentation between *P. tridentatum* var. *crassifolium* and *P. leptophyllum* are not valid. Evidence based on morphology, ecology and flowering time indicate that all of the specimens from eastern Baja California and adjacent islands should be included under *P. tridentatum* var. *crassifolium*.

REPRESENTATIVE SPECIMENS: BAJA CALIFORNIA. 20 mi s of Muleje, 14 Nov 1946, *Wiggins 11404* (UC). Bahia Conception, 35 mi s of Muleje, 15 Mar 1935, *Shreve 7102* (F, MICH). Tiburon Island, 11 Apr 1911, *Rose 16772* (GH). Carmen Island, Puerto Ballandra, 21 May 1921, *Johnston 3815* (GH, UC, US).

EXCLUDED NAMES

1. *Porophyllum cacalioides* (Less.) DC., Prodr. 5:650, 1836. This species is from the Philippines and pertains to a genus unknown to me.
2. *Porophyllum caesium* Casar., Nov. Stirp. Bras. Dec. 86; 1845. Not *P. caesium* Greene; 1911. This species was described and reported from Brazil without designation of type or citation of specimens, and it was not included by Martius (1884) in the Brazilian flora. It is known to me only as an obscure name.
3. *Porophyllum cusimbua* (Don) DC., Prodr. 5:650, 1836; is *Gynura angulosa* DC., Prodr. 6:298, 1837.
4. *Porophyllum japonicum* DC., Prodr. 5:650, 1836; is *Gynura pinnatifida* DC., 6:301, 1837.
5. *Porophyllum oppositifolium* DC. is based on *Cacalia oppositifolia* Poir., Suppl. 2:7 *in* Lam. Encycl. Meth., 1811. The specimen in the Candolle Prodromi Herbarium (Photograph, KANU) has no involucres and is of unknown taxonomic position.
6. *Porophyllum selloi* (Spreng.) DC., 5:651, 1836; is *Stevia oxylaena* DC., 5:123, 1836.

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● P. ruderale subsp. macrocephalum

FIGURE 11

● P. ruderale subsp. ruderale
▲ P. leiocarpum

FIGURE 12

● P. lanceolatum
■ P. hasslerianum
□ P. oppositifolium
○ P. linifolium
▲ P. angustissimum

FIGURE 13

FIGURE 14

FIGURE 15

● P. pringlei
■ P. calcicola
▲ P. quinqueflorum

FIGURE 16

■ P. coloratum
● P. obtusifolium
▲ P. warnockii
□ P. tagetoides
○ P. filiforme
△ P. linaria

FIGURE 17

△ P. gracile
○ P. greggii
□ P. brachypodum
▲ P. amplexicaule
● P. scoparium
■ P. pausodynum

FIGURE 18

▲ P. t. tridentatum
● P. t. crassifolium
■ P. maritimum and P. porfyreum

FIGURE 19

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Reptiles from the Mariana and Caroline Islands

G. L. DRYDEN[1] AND EDWARD H. TAYLOR[2]

This paper records eleven previously described species of lizards and four previously described species of snakes collected by one of us (Dryden) from June, 1962 to May, 1964 in the Mariana and Caroline Islands. In addition, a presumed new species of typhlopid snake from Guam, Mariana Islands is described. The lizards include one rather rare gekkonid (*Peropus papuanus*) from Angaur, West Caroline Islands and Saipan, Mariana Islands as well as two unusual skinks (*Mabuya multicarinata* and *Eugongylus mentovarius*), both from Angaur, West Caroline Islands. Also included is a group of *Dasia smargdinum* of questionable subspecific designation from Ponape, East Caroline Islands. No amphibians were collected although the recently introduced toad, *Bufo marinus* was abundant on Guam, and to a lesser extent, on Saipan.

We thank Carl Dannis for capturing the *Dasia* on Ponape and Dr. K. R. Barbehenn for taking the new form of *Typhlops* on Guam. Henaro Sabino helped collect on Guam and Koror, Palau, as did Tasiano Marar on Angaur, Palau.

The numbers, referred to below, pertain to specimens now in the Edward H. Taylor-Hobart M. Smith (EHT-HMS) collection, Department of Zoology, University of Kansas.

Typhlops braminus (Daudin)

Eryx braminus Daudin, 1803, Histoire naturelle des reptiles, 7:279-280 (Based on Russell, 1796, Ind. Serp., 1:48, pl. 43; type-locality, Vizagapatam, India).

Two of our nine specimens were taken on a military area on northern Saipan, the others from the northern half of Guam. A partially digested specimen was recovered from the stomach of a *Varanus indicus indicus* taken in the latter area.

[1] Department of Biology, Slippery Rock State College, Slippery Rock, Pennsylvania 16057.
[2] Department of Zoology, University of Kansas, Lawrence, Kansas 66044.

The species has been collected on several other islands in the Marianas and we presume that they occur on all. They are, however, smaller in size than those of populations occurring in continental Asia and certain larger islands of the Indo-Australian Archipelago. The maximum and minimum lengths occurring in our series are 127 mm and 58 mm, respectively.

Typhlops pseudosaurus sp. nov.

TYPE: EHT-HMS No. 6717, collected at Harmon Village, Guam, Mariana Islands, March 30, 1963 by Dr. K. R. Barbehenn.

DIAGNOSIS: A diminutive species, the type specimen being 82 mm in length; rostral fails to reach eye level by a distance half the length of dorsal portion of rostral; nasal completely divided; eyes visible; prefrontal and frontal relatively large; 20 longitudinal scale rows at middle of body; 318 transverse scale rows following parietals, followed by terminal spine.

DESCRIPTION OF THE HOLOTYPE. Rostral moderately narrow, failing to reach back to level of eyes by a distance equal to four fifths of length of prefrontal; nasals separated by prefrontal, which is a little wider than long; frontal minutely larger than prefrontal and following interparietal. Rostral dorsally slightly less than one-third of width of head. Supraoculars somewhat diagonally placed, the outer edge barely touching upper part of eye, which is covered by ocular; interparietal not larger than the two pairs of parietals, which touch it. Nasal completely divided, the suture arising from preocular; four supraoculars increasing in size from first to fourth; a single postocular between fourth labial and parietal; 20 longitudinal scale rows and 318 transverse rows following parietals. Vent bordered anteriorly by five semitransparent scales, the two outer twice the transverse width of the others; 12 longitudinal subcaudal rows+1 (spine).

Color: Light blue dorsally and ventrally in life. After fixation in formaldehyde and storage in ethanol, silvery gray above and vaguely lighter silver below. Lower jaw, chin, and upper labials cream. Tip of snout whitish, gradually becoming grayish above. Terminal spine creamy white.

Measurements in mm: Total length, 82; tail length, 2; width of head, 2.

Remarks: The specimen was obtained in an area where *Typhlops braminus* also occurs. There is an obvious difference in color, but in certain brown species of *Typhlops,* the specimens just before shedding are often grayish or silvery gray and we suspect that the silvery color of our specimen might be less pronounced after shedding.

The glandules below the head sutures always present in *T. braminus* are seemingly completely absent in the form here described. The presence of a shortened rostral easily separates it from *T. braminus.*

Enygrus carinatus (Schneider)

Boa carinatus Schneider, 1801, Historiae amphibiorum naturalis et literarie, Fasc. 2, p. 261-263 (type-locality unknown).
Enygrus carinatus, Duméril and Bibron, 1844, Erpétologie générale, 6:479-483.
Enygrus superciliosus Günther, 1863, Ann. Mag. Nat. Hist., ser. 3, 12:360-361, pl. 6, fig. D (type-locality "Pelew Islands").

Two specimens were taken in the Palau Islands group, one on Koror and one on Angaur. The specimen from Koror is adult. The scale formula is 31-34-23; there are 180 ventrals, 45 single subcaudals. The specimen is a female and contains three embryos. A fourth embryo seemingly had died and had been partly resorbed before capture of the specimen. The specimen taken on Angaur is a much younger one and very much lighter in color.

Günther, with two specimens from the Palau ("Pelew") Islands, described *Enygrus superciliosus,* which was later placed in the synonymy of *E. carinatus* by Günther and others.

Dendrelaphis lineolatus Hombron and Jacquinot

Dendrelaphis lineolatus Hombron and Jacquinot, 1842, Voyage au pôle sud et dans l' oceanie sur les corvettes l'Astrolabe et la Zélée, III. Reptiles, p. 20, pl. 2, fig. 1 (type-locality ?); Duméril, Bibron, and Duméril, 1854, 7(I):200 deal with the species *Dendrephis lineolata* Nobis. "Cette espèce inédite, dont nous possédons plusieurs individus, proviennent, les uns de MM. Hombron et Jacquinot, et ils sont figurés dans le voyage de Dumont d'Urville en 1842, et décrits dans la relation de ce voyage par M. Guichenot. Les autres ont été recueillis probablement à la Nouvella Hollande par M. J. Verreaux, par M. Freycinet, et par MM. Quoy et Gaimard, en 1824, dans les îles Waigiow."

Three specimens were captured in the Palau Islands. Since these have been preserved in formalin the original color and markings are largely obliterated. The variation in squamation and measurements is shown in Table 1. The temporals are somewhat variable and the preocular reaches but only touches the frontal (on one side). The sixth labial has a posterior, elevated point suggesting that a postocular has been fused with it.

TABLE 1. Data on *Dendrelaphis lineolatus.*

Number	17	18	19
Locality	Koror, Palau	Angaur, Palau	Angaur, Palau
Body length	764	655	710
Tail length	363	318	333
Total length	1127	973	1043
Ventrals	180	176	184
Subcaudals	129—	138	132
Scale formula	15.13.11	15.13.11	15.13.11
Supralabials	9-9	9-9	9-9
Supralabials in orbit	5,6	5,6	5,6
Infralabials	10-10	9-10	10-10
Infralabials touching chinshields	5-5	5-5	5-5

Boiga irregularis Merrem

Coluber irregularis Merrem, 1802, *in* Bechstein, Uebers. Lacépède, 4:239, pl. 37, fig. 1 (type-locality ?) [publication not seen].

Three specimens of this species taken in Guam are present in the collection. Two (Nos. 6720 and 6722) are complete; one (No. 6721) consists of a head and the anterior part of the body. See Table 2.

TABLE 2. Data on *Boiga irregularis*.

Number	6720	6722
Body length	971	782
Tail length	276	219
Total length	1247	1002
Supralabials	9-9	9-9
Supralabials entering orbit	4,5,6	4,5,6
Infralabials	13-14	13-14
Scale formula	23,23,19	23,23,19
Anal	1	1
Ventrals	257	257
Subcaudals	116+1	116+1

Lepidodactylus lugubris (Duméril and Bibron)

Platydactylus lugubris Duméril and Bibron, 1836, Erpétologie générale, 3:304 (type-locality "cette petite espèces a été raportée de l'île d'Otaïte" [=Tahiti]).

Our specimens are from the following localities: Nos. 6755, 6758, Guam, May 10, 1963; 6759-6764, Saipan, Aug. 4 to Sept. 28, 1962; 6752-6758, Angaur, Palau, June, 1964. These show a minimum of variations except for four specimens, one from Guam (No. 6755) and three from Saipan (Nos. 6759-6761). These have retained the transverse bands on the body and tail and much pigmentation on the head, including a scattering of pigment on the chin. These markings are strongly reminiscent of the pattern of *Lepidodactylus woodfordi* Boulenger (Boulenger, 1887). None of the specimens mentioned above has preanal or femoral pores and it is presumed that all are females. The males, of which only a few have ever been seen or taken, are said to have a long series of about 25 femoral pores, which are angular in the middle. The "pore scales" of our females number only 7 to 9.

Hemidactylus frenatus Schlegel *in* Duméril and Bibron

Hemidactylus frenatus Schlegel, 1836, *in* Duméril and Bibron, Erpétologie générale, 3:366-368 (type-locality, Java).

Concerning the type, Duméril and Bibron state: "Le nom de *Frenatus,* qui nous a servi pour désigner cette espèce, est celui sous lequel elle nous a été envoyée d'Musée de Leyde." However, numerous other specimens were

available to these authors. They mention specimens from Madagascar, Ceylon, Amboina, Java, Timor, Bengal, and "'Nous en avons plusieurs échantillons recueillis aux îles Mariannes par M. Gaudichaud." Schlegel's specimen came from Java.

A large series of about 150 specimens of this species from Guam were preserved. They were very common. Specimens also were obtained on Saipan in the Marianas and on Angaur in the Palau Islands.

Cagle (1946) reported a gekkonid lizard as being used in Tinian for field studies, together with geckos belonging to two other genera. He states that "*Hemidactylus*, the most abundant form, was studied by marking." The species was reported as *H. garnotii*.

We feel almost certain that the material so used was *Hemidactylus frenatus* that had been incorrectly identified for Dr. Cagle. It has not been possible to verify this opinion as his specimens seemingly were lost in the mails.

Apparently no other collector has found *H. garnotii* in the Marianas. It would not be surprising that it did occur but not to the exclusion of the much more common *H. frenatus*.

Gehyra oceanica (Lesson)

Gekko oceanicus Lesson, 1830, Voyage autour du monde éxécute par ordre du Roi sur la corvette de sa Majesté La Coquille, pendant les années 1822-25, Zoologie, Lesson and Garnot, 2(1):42, pl. 2, fig. 3 (type-locality "Des îles d'O-Tahiti et de Borabora"); Brongersma, 1934, Zool. Meded., 17:174.

This species is represented by one adult specimen and a juvenile from Saipan, Mariana Islands.

The lamellae under the digits are transverse, and completely undivided. The species has been reported previously from the Marianas. It is widespread in New Guinea and the numerous Island groups to the west, northeast, and southeast, but does not extend to the east as far as the Marquesas Islands.

Peropus mutilatus Wiegmann

Hemidactylus (Peropus) mutilatus Wiegmann, 1835, Nova Acta Acad. Caes. Leopoldino-Carolinae Nat. Cur., 17(1):238 (type-locality "cette espèce a été trouvée à Manille).

Two specimens (Nos. 6705 and 6706) of this wide-ranging species were taken on Angaur in June, 1963. The count of femoral pores is 16-15 and 18-16, respectively.

Peropus papuanus A. B. Meyer

Gehyra papuana Meyer, 1874, Monatsb. Kgl. Akad. Wiss. Berlin, p. 129 (type-locality New Guinea); Sauvage, 1878, Bull. Soc. Philom. Paris, ser. 7, 2:31; Brongersma, 1934, Zool. Meded., 17:174-175.

Gehyra oceanica (part.), Peters and Doria, 1878, Ann. Mus. Civ. Genova, 13:369; Boulenger, 1885, Catalogue of the lizards in the British Museum, 2nd ed., 1:152-153.

The type-description of this form follows: "Steht *G. australis* Gray nahe. Über den Ohren und hinter den Augen eine dreieckige, nach oben spitze Hautfalte. Purpur-grau. Unterseite kaum heller gefärbt. Kinnschilder 3.3. Femoralporen vereinigen sich bogenförmig in einem mit den Spitze nach vorn gerichten *v* mit den Präanalporen."

This brief description caused certain subsequent authors to place *papuanus* in the synonymy of *Gehyra oceanica*. Brongersma (*loc. cit.*) who has studied the type, has shown that it is indeed a species distinct from *oceanica*. He presents a satisfactory redescription of the type.

A specimen (No. 6699) taken in Angaur, one of the southern islands of the Palau group, which lies almost directly north of the western end of New Guinea, has been referred to *Peropus papuanus* Meyer.

The head is slightly shorter proportionally and there are fewer labials than in the type. The character of the digital lamellae, the squamation, skin folds on the side of the body and head, etc. are much the same as reported by Brongersma for the type. Our specimen has lost its tail.

Two other specimens were obtained in Saipan, Mariana Islands (Nos. 6697 and 6698). In these the heads are proportionally longer. The preanal pores or pore scales (they scarcely reach the femoral region) are 8-11, 9-8, a much smaller number than is reported for the type of *papuana*.

Whether there are other significant differences that might warrant subspecific designations for these island forms can only be determined by their direct comparison with the type of *Gehyra papuana* Meyer, with the type of *Peropus lampei* Anderson from Bogadjim, New Guinea, and with the type of *Peripia papuensis* Macleay from Katow, New Guinea.

Gekko vittatus bivittatus (Duméril and Bibron)

Platydactylus bivittatus Duméril and Bibron, 1836, Erpétologie générale, 3:334 (type-locality "l'un de la nouvelle-guinee, l'autre de l'ile Waigiou").
Gecko vittatus bivittatus Boulenger, 1885, Catalogue of the lizards in the British Museum, 1:186-187.

Three specimens (Nos. 6702-6704) are from Angaur, Palau Islands, in the West Caroline Islands. The specimens are typical as regards most characters. The two males have a count of 23-23 and 15-17 femoral pores. Boulenger has previously reported the species from the "Pelew Islands." It is distributed rather widely in the western Pacific Islands.

Mabuya multicarinata (Gray)

Tiliqua multicarinata Gray, 1845, Catalogue of the specimens of lizards in the collection of the British Museum, p. 109 (type-locality, Philippines).
Mabuia multicarinata, Boulenger, 1887, Catalogue of the lizards in the British Museum, 2nd ed.,

3:185, pl. XI, fig. 2; De Rooij, 1915, Reptiles of the Indo-Australian Archipelago, 1:161; Taylor, 1922, The lizards of the Philippine Islands, Manila, pp. 156-158, text fig. 13, pl. 12, fig. 2.

The distribution of this species in the Indo-Australian Archipelago, Philippines, and the Islands of the western Pacific is rather spotty. De Rooij mentions specimens only from Kina Balu (Mt.) Borneo and Karakelang Islands. One of us (Taylor) has reported it throughout the Philippines.

The series at hand is from the Palau island of Angaur. The series differs from many Philippine specimens in having the parietals separated by the interparietal. Table 3 presents much of the variation in this species.

The females show a stronger dark lateral stripe than the males, and most of them have several narrow, dark, more or less distinct longitudinal lines on the dorsum. In all, the soles of the feet are creamy white while the underside of the digits is blackish. In all, the rostral touches the frontonasal, which in turn is in contact with the frontal. There are six or seven keels on most dorsal scales. Beginning at the 20th subcaudal the scales are strongly widened. There are about seven preanal scales, the two median a little the larger and all light cream or yellowish in color.

The upper palpebral scales are distinctly larger than the lower palpebrals.

TABLE 3. Data on *Mabuya multicarinata*.

Number	6775	6777	6778	6779	6782	6784	6785	6786	6789	6788	6790
Sex	m	f	f	m	m	m	m	m	m	m	m
Body length	64	64	67	70	64	79	66	65	68	77	77
Tail length	107	126	inc	91+	123	123	111+	inc	inc	128	inc
Scale rows at middle	30	30	30	30	30	30	30	30	30	30	30
Scales (parietals to above vent)	45	43	43	43	43	43	42	43	43	43	44
Subcaudals	91+	99	?	66+	91	93	inc	?	inc	82+	inc
4th finger lamellae	17	16	17	16	17	17	17	17	17	16	17
4th toe lamellae	25	24	25	24	24	23	25	25	25	25	25
Supraciliaries	5	5	5	5	5	5	5	5	5	5	5

Carlia fuscum (Duméril and Bibron)

Heteropus fuscus Duméril and Bibron, 1839, Erpétologie générale, 5:759-760 (type-locality, "Cette espèce a été trouvée dans les îles de Waigiou et de Rawack par MM. Quoy et Gaimard") (here restricted to Waigiou [Waigeu]).

Three specimens of *Carlia fuscum* were taken, presumably a species that has not been reported in the Marianas previously. One of the specimens (No. 6728) was caught in a mousetrap at night at the Kobler Air Field in south Saipan, the other two (Nos. 6726 and 6727) were found in a meadow south of the village of San Roque, Saipan.

The species was relatively common; several other specimens were seen running on grass or other vegetation above the ground.

Counts of the scale rows about the bodies are 32, 32, 34; the counts of the lamellae under the fourth toe are 33, 31, 26, respectively.

We have utilized Gray's genus *Carlia* for this species, characterized by an undivided frontoparietal, a very small interparietal, and the digital formula 4-5.

Eugongylus mentovarius (Boettger)

Lygosoma (Riopa) mentovarium Boettger, 1895, Zool. Anz., no. 471-472:4-6 (type-locality, Halmahera Island).

A large specimen (No. 6729) of this skink, taken on Angaur, Palau, West Caroline Islands, has the following characteristics:

DIAGNOSIS: Frontoparietals paired and supranasals present; limbs well developed, overlapping when adpressed; lower eyelid scaled.

DESCRIPTION: The snout short and blunt; rostral moderately large, well visible from above, making a narrow contact with frontonasal; frontal narrower than frontonasal but considerably longer, forming a suture with it; prefrontals small, widely separated. Four large supraoculars, the area occupied by them a little narrower than the frontal. Frontoparietals paired, interparietal equally as large or larger than frontoparietal. Parietals large, enclosing interparietal; one pair of enlarged nuchals. Nasal small, partly or entirely divided, about size of supranasal; nostril surrounded by 3 scales; 2 frenals, the anterior the higher, bordering prefrontal; in superimposed pair of preoculars directly below first supraciliary, which is largest of a series of 8. A row of 7 pre- and postsuboculars separates the eye from the labials. Two small superimposed primary temporals followed by 3 secondary temporals, the upper much the larger. Five supralabials precede the somewhat enlarged subocular and 2 follow it, while on lower jaw, there are 6 infralabials. Mental narrow and considerably wider than rostral, followed by a much larger undivided postmental; a pair of chinshields touching labials. Subsequent chinshields separated from labials. Ear moderately large with 3 or 4 small, projecting lobules.

Body moderately slender, limbs robust. When adpressed, fourth toe reaches fingers of adpressed arm. Distance from tip of snout to insertion of arm is contained in axilla to groin distance about 1.4 times. Fifteen lamellae present under both third and fourth fingers, and 25 under fourth toe. There are 12 preanal scales, the 2 median, somewhat enlarged. Scale rows around neck, about 38; around middle of body, 32; anterior dorsal scales largest; 75 scales in a row from parietal to above vent; 143 subcaudal scales from vent to tip of tail.

General color brownish olive on dorsum and sides of body and tail; top of head uniform brown. Underside of head, body, limbs, and tail ivory yellow; undersurface of hand and foot blackish except first finger and toe

which is yellowish. Brown marks cross labials and mouth angles and bend back on chin and throat for some distance. Median dark line behind occiput for about 1 inch, while crossing neck and body are about 15 series of irregular black dots and scattered lighter olive spots indicative of transverse bands. A few can be discerned on basal half of tail. A few vague darker marks apparent on side of neck.

Measurements in mm: Snout to vent, 127; tail, 208; total length, 330; width of head (greatest), 18; tip of snout to ear-level, 22.5; snout tip to arm insertion, 46; axilla to groin, 65; arm, 32; leg, 46.

Remarks: We have associated this species with the genus *Eugongylus* Fitzinger. Smith (1937) considered it as a sub-genus under *Riopa*. Mittleman (1952), a separate genus.

Cryptoblepharus poecilopleurus (Wiegmann)

Ablepharus poecilopleurus Wiegmann, 1835, Nova Acta Acad. Caes. Leopold-Carol., 17(I):202, pl. 8, fig. 1 (type-locality ?).

Our specimen (No. 6742) was captured on Saipan on Sept. 28, 1963. Six others (Nos. 6743-6748) are presumably also from Saipan. The data accompanying them were lost in shipment.

Specimen No. 6742 has the following characters: rostral in contact with large frontonasal; supranasals lacking, prefrontals large, forming a median suture; frontal narrower than suprocular area, its length about half length of single frontoparietal, which is enclosed by parietals. One pair of large nuchals and a pair of large temporals border posterior edges of parietals. Four supralabials precede the subocular, fourth very small; mental has a larger labial border than rostral; postmental and 3 large pairs of chinshields border infralabials, of which there are 6.

There are 24 scales about middle of body and 21 lamellae under fourth toe. Eye circular, without lids, incompletely surrounded by several circular rows of minute scales. Three small scales between eye and supraciliary scales; 2 median dorsal scale rows are largest at first, almost as wide as the nuchal, then gradually diminishing in width posteriorly; preanal scales distinctly enlarged and subcaudal series wider than adjoining rows. The series has a size range from 26 mm to 37 mm in body length. When limbs are adpressed, fourth toe reaches a little beyond elbow.

We believe that this species has heretofore not been reported from the Marianas.

Dasia smaragdina viridipunctum (Lesson)

Scincus viridipunctum Lesson, 1830, Voyage autour du monde exécuté par ordre du Roi sur la corvette de sa Majesté, La Coquille, pendent les années 1822-1825, Zoologie, 2(1):44, pl. 4, fig. 1 (type-locality Oualan [=Kusaie], Eastern Caroline Islands); Barbour, 1912, Mem. Mus. Comp. Zool. Harvard College, 44(1):91-92, pl. 1, figs. 1 and 2; pl. 2, fig. 4.

A series of specimens (Nos. 6792-6811) is from Ponape, Eastern Caroline Islands. They agree with one of the forms described from "Oualan" by Lesson under the above name. Another species called *smaragdina* was described in the same publication from the same locality but subsequent collecting in the Carolines has failed to rediscover this form that is often very numerous in other localities. Barbour suggests that the type of *D. smaragdina* is not from the Carolines, but due to an error in labelling, was so reported. Lesson also reported this form in the Palau (Pelew) Islands. A second series (Nos. 6812-6826) from Angaur, Palau, Western Carolines, differs somewhat in coloration from the Ponape series. In the second series, almost all the scales on the dorsum have darker areas or darker borders which form an indefinite series of five or more dim longitudinal lines from head to the base of the tail, the lines often connected with each other with narrow black, very irregularly placed, dashlike marks.

Emoia werneri Vogt

Emoia cyanurum var. *werneri* Vogt, 1912, no. 1, Sitzungsb. Gesel. natur. Freunde Berlin, p. 5 (type-locality "Marianen").

Six adult specimens and four young (three from eggs) were collected on Guam. The young show the three light lines quite clearly. In adults these lines fade and are absent or difficult to see, especially in male specimens. The lamellae under the fourth fingers vary from 24 to 28; under the fourth toes from about 39 to 41.

A series of five specimens was taken on Angaur in the Palau Islands. In these specimens the stripes were distinct anteriorly in the adults. The lamellae under the fourth finger varied from 25 to 28; under the fourth toe from 40 to 44.

In the Guam specimens the postaxillary scales were typical of scales elsewhere on the body but in the Angaur specimens they were modified to form chigger-mite refuges. In these, the scales were juxtaposed or barely overlapping, thus allowing space for the mites to attach to the flesh between scales. Numerous parasites were present on each side of each specimen. In two specimens a pair of symmetrical "postparietal" scales separated the parietals, and in a third specimen a suture partially severed the posterior part of one of the parietals. The other two specimens had typical parietal scales forming a suture.

Varanus indicus indicus (Daudin)

Tupinambis indicus Daudin, 1802, Histoire naturelle, générale et particulière des reptiles, 3:46-47, pl. 30 (type-locality "découvert dans l'île d'Amboine, par Riche").

Varanus (Varanus) indicus indicus, Mertens, 1942, Abh. Senckenb. naturf. Gesell., Abh. 466:263-270 (see pl. 6 in Mertens, 1942, ibid. Abh. 462:1, for variation in markings).

This species was relatively abundant on Guam, especially in the northern half of the island, and is found on various other islands in Micronesia (Dryden, 1965). One hundred specimens (54 male, 42 female, and 4 of undetermined sex) were caught or shot on the northern half of Guam. Total length and tail length ranges in mm are 305-1330 and 183-749, respectively.

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Miscellaneous Notes and Descriptions of New Forms of Caecilians[1]

EDWARD H. TAYLOR[2]

The following notes were prepared to be published as a supplement to my treatise on the caecilians of the world. This was found to be impractical so they are offered herewith.

In regard to the description of *Caecilia gracilis* and *Microcaecilia unicolor* in that work, one figure has been erroneously labeled and certain data omitted. The corrections are contained herein.

In addition, on a recent visit to the Berlin Museum, the type of *Oscaecilia polyzona* (Fischer), believed to have been lost, was found in a container under another name. Data are given on this specimen.

Finally, two new species and two new subspecies are described.

In the preparation of these notes, I placed myself under obligation to several persons. I offer my gratitude to the following: to Dr. George S. Myers for the loan of a specimen of *Oscaecilia ochrocephala*, var. and to its collector, Mr. John S. Applegarth; to Dr. Gaston Françoise de Witte of the Institut Royal des Sciences Naturelle de Belgique who arranged the loan of Congo materials; to Dr. J. Guibé for the loan of the *Ichthyophis laosensis* from the Museum Nacional d'Histoire Naturelle, Paris; to Dr. Charles M. Bogert, American Museum of Natural History, for the loan of the Ceylon specimen; and to Dr. Günther Peters and Mr. Peter Buerton of the Berlin Museum for the opportunity to study the type of *Oscaecilia polyzona*.

Caecilia gracilis Shaw

In my *Caecilians of the World: A Taxonomic Review* (Taylor, 1968), due to a metathesis of data and plates, I have labeled Fig. 200, p. 384, "*Caecilia gracilis* Shaw, Field Museum of Natural History No. 35116, Arenoque, British Guiana." This is entirely erroneous. The specimen figured is actually

[1] This work has been pursued under grant No. GB 4510 of the National Science Foundation.
[2] Research Associate, University of Kansas Museum of Natural History.

Field Museum of Natural History No. 35117, *Microcaecilia unicolor* A. Duméril, from Oko River, Cuyoni River, British Guiana, Neal A. Weber collector, June, 1936.

The description of the species, p. 389, is actually taken from a specimen of *Caecilia gracilis* which bears the Field Museum of Natural History Museum No. 35116 from the Arenoque River, British Guiana, 2° 42′ N Lat. "In a shovel of sand at water level."

On p. 391 of the description one finds: *"Measurements:* See Table." Owing to the original size of the Table, it was necessary to strike off a part of the data recorded for other specimens and inadvertently the data for the described specimen (No. 35116) was not included.

The following data apply to the specimen described: total length, 283 mm (body somewhat elastic); head width, 4 mm; body width, 4.2 mm; tentacle to eye, 1.9 mm; tentacle to nostril, 0.8 mm; first collar indistinct (because of abnormal swelling); second collar moderately distinct, fused ventrally with first primary fold; snout-tip to first nuchal groove, 5.1 mm; to second groove, 6.8 mm; to third groove, 8.6 mm (lateral measurements). Primary folds, 198± (difficult to count in certain parts); secondaries, 23, 7 complete; eye hidden under skin, but situated in a socket 1.9 mm from tentacle; nostril from tentacle, 0.8 mm; nostrils distinctly visible from directly above head; tentacle, not visible from above, is below nostril and vaguely in advance of nostril. Choanae relatively large, the diameter of one choana in the distance between them, 1 time.

Premaxillary-maxillary tooth series, 9-1-9; prevomeropalatine series, 9-1-9; dentary, 10-10, the anterior dentary teeth the largest in mouth; splenial, 2-2. Scales present in folds in a single row. These first appear near point where secondaries make their first appearance. Posteriorly there is still only a single row in each fold. These are large, subcircular overlapping scales. No subdermal scales found.

Oscaecilia polyzona (Fischer)

Caecilia polyzona Fischer, *in* Peters, 1879, Monatsb. Akad. Wiss. Berlin, p. 936; Fischer, 1880, Arch. für Naturg. Jahrg. 46(1):215, pl. 8, figs. 1-4.

The two cotypes of this species, collected by Grosskopf at Cáceres, Antioquia, Colombia were originally in the Kön. Zool. Museums in Berlin. One of these was acquired by the American Museum of Natural History. The other specimen was presumed to be absent from the Berlin collection in 1929 and reported "whereabouts unknown."

In studying material in the Berlin Museum, now called Zoologisches Museum der Humboldt-Universität, I found the second cotype masquerading under another name, seemingly having been placed accidentally in a wrong container. Since I name this the lectotype, I present the following data on the specimen.

The specimen now bears the number 9524 and was collected by Grosskopf in Antioquia, Colombia. Fischer gave a more complete description in 1880 than that given in Peters' paper the preceding year.

The specimen is female and somewhat softened so that its present measurement of 712 mm (stretched to eliminate the sinuosity of the spine) is considerably larger than Fischer's measurements of 650 or 670 mm for the two cotypes.

Primary folds 210, and 15-16 secondaries with at least two complete. Collars both complete, each with a dorsal transverse groove. Eye solidly covered by bone. Aperture of tentacle relatively far from edge of lip; nostrils plainly visible from directly above head; choanae rather large, circular, the diameter of one in the distance separating them about 2 times; tongue with two well-developed narial plugs; a very small terminal "shield." Snout projects somewhat beyond mouth with a rather sharp transverse edge.

The tooth counts are: premaxillary-maxillary series, 6-1-6, anteriorly very large, diminishing somewhat laterally, teeth bent backwards; prevomeropalatine, 11-1-12; dentary, 11-11; splenial, 4-3.

These do not correspond exactly with tooth counts of Fischer. He states 22-25 teeth in the gums and, in a parallel row, about 20-22 in the lower jaw, first row; in the second, 10-12. All teeth bent back.

Of the secondaries, Fischer states that on the last 10 or 12 folds there are accessory rings inserted which first appear in the dorsolateral region, then on the sides and finally reach to the middle of the venter. His count of the primary folds is 209 and 207.

In the museum in Vienna there is a specimen of this species (No. 9141) from Cárceres, Antioquia, Colombia, collected by Grosskopf (in 1880?). This seemingly topotypic specimen was probably not seen by Fischer.

Oscaecilia ochrocephala var.

(Fig. 1)

Thanks to the kindness of Dr. George Myers, I have examined a specimen of caecilian from the Canal Zone, Panamá, collected by Mr. John S. Applegarth which although having certain characters of *Oscaecilia ochrocephala* and occurring in an area where typical *O. ochrocephala* are to be found, differs markedly in several characters. While these differences are largely of size and markings, it is worth while to put the specimen on record.

The distribution of *O. ochrocephala* is rather limited, being confined, so far as known, to the State of Panamá and the Canal Zone. *Oscaecilia polyzona* is a closely related form, three specimens of which are known from Colombia. Other members of the genus are scattered, chiefly in the northern part of South America.

The specimen, Stanford University Division of Systematic Biology Museum, No. 21864, was collected just behind the Latin American School at the

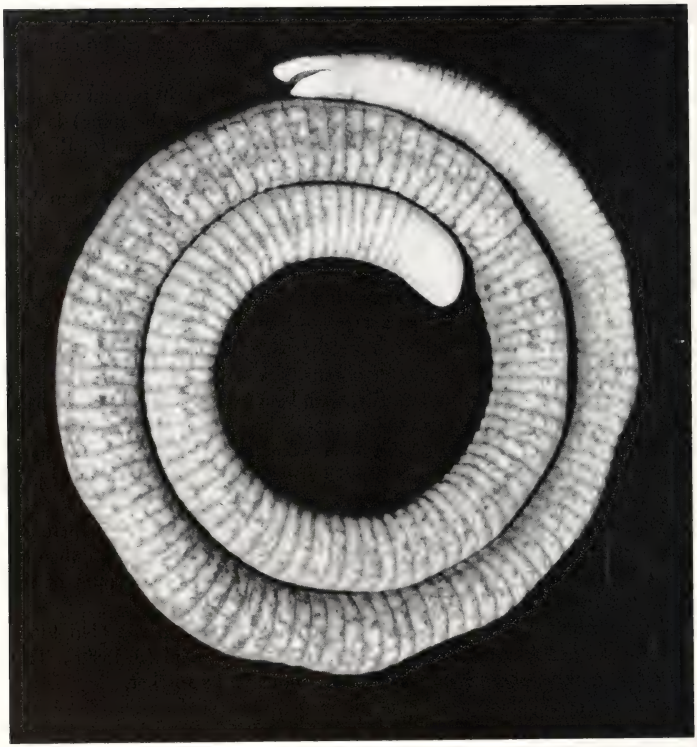

FIG. 1. *Oscaecilia ochrocephala* var. Stanford Museum, No. 21864, Albrook Air Force Base, Canal Zone, Panamá. Total length of specimen (before preservation), "62 cm"; present length, 520 mm. Lateral view.

Albrook Air Force Base on May 30, 1965 by John Applegarth (Fig. 1). The data associated with the specimen state, "60 cm in length before formalin."

The specimen is described as follows: head tapering, the snout oval seen from above, extending beyond the mouth 3.1 mm. Eyes under bone, not visible externally; nostrils well visible from directly above head; tentacle in a tiny depression almost directly below nostril, closer to it than to lip, and not visible from above head. First collar well defined, with a dorsal groove; first and second nuchal grooves visible ventrally, the first less distinct than second. Second collar relatively narrow, a transverse groove above, fused to the first primary ventrally. Primary folds, 181, complete above and below. Small

terminal shield, somewhat pinched or flattened; secondaries, 9, none complete ventrally. Vent small, transverse or subcircular. Denticulations small, about 7 anterior and 8 posterior to vent. A pair of small anal glands precede vent on denticles.

The dentition: premaxillary-maxillary teeth, 7-1-7; prevomeropalatine, 11-1-10; dentary, 10-10, the posterior 5 of series very small, the anterior ones the largest in mouth; splenials, 2-2. Tongue with two small narial plugs, choanae small. Maxillary tooth series reaches barely beyond level of choanae.

Scales present beginning at second sixth of body length, the scales at first very small, 0.1 to 0.5 mm in greatest width; in the last centimeter they vary between 1.6 to 2.0 mm in largest measurements. Many scales nearly quadrangular with a slight elevation near the center.

Total length now 520 mm (620 before preservation), the spine, now sinuous since preservation. Head width, greatest, 9.5 mm; width of body for most of its length, 15 mm; width one cm before terminus, 14.4 mm; snout tip to first groove, 11.3 mm (lateral measurements); to second groove, 14 mm; to third groove, 17 mm. Width in length, 34.6 (or 41) times.

Color of preserved specimen generally slate, the grooves very faintly darker. Venter and lower sides grayish with yellowish-gray spots and irregular flecks. Head much lighter slate than body, with two light lateral areas including lip and snout tip. Lower jaw yellowish; chin dark. Area about vent whitish.

Of the more than 100 specimens from which data have been taken, or on which data have been published, eight specimens are measured above 500 mm and, of these, only one measures above 600 mm (610 mm). The greatest body width recorded for these eight specimens is 12 mm for the 610 mm specimen; four have a measurement of 10 mm, one of 11 mm and one of 7 mm. The width-in-length ratio is smaller in this specimen than in all others.

The color generally is different from the usual specimens of *O. ochrocephala*, in which the folds have very definite black-barred primary grooves and the body is not mottled.

It is possible that other specimens having these characteristics are among the specimens reported in the literature. It is also quite possible that the skull may show still other differences.

Geotrypetes congoensis Taylor

(Figs. 2-3)

Geotrypetes congoensis Taylor, 1968, Caecilians of the World: A Taxonomic Review, pp. 715-718, figs. 392-393.

The accompanying Figs. 2-3 were prepared to amplify Fig. 393 of the cited work.

Characteristic scales of this species taken from the posterior dorsal part of the body are also shown here. The scales measure 1.7 × 1.2 and 1.7 × 1.0 mm.

FIG. 2. *Geotrypetes congoensis* Taylor, Musee Royal de l'Afrique Centrale, Belgium, No. 101464. Kitadi, Mayumbe Region, Kivu, Belgian Congo, Africa. Actual width of head at first nuchal groove, 5 mm. Type. Dorsal, lateral, and ventral views of head; dorsal and ventral views of terminal area.

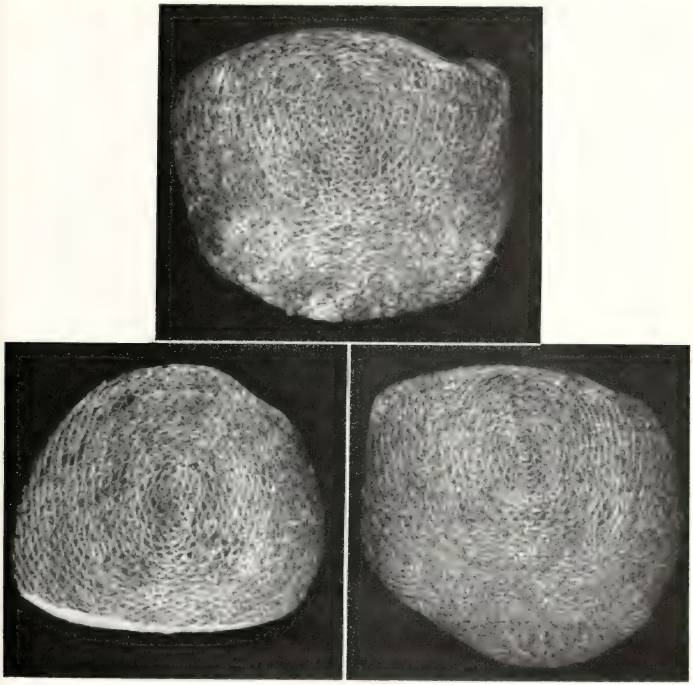

FIG. 3. *Geotrypetes congoensis* Taylor. Type. Scales from the folds of the last centimeter of body. Largest scale measures 1.7 × 1.2 mm.

In the posterior folds there are 6-7 rows of scales; the uppermost of the series may be smaller than those depicted here.

Hypogeophis rostratus lionneti subsp. nov.*

(Fig. 4)

TYPE. Nairobi National Museum, No. A-602, "Seychelles."

The various forms of *Hypogeophis* have been recognized as subspecies by Parker (1958). The specimen here described is placed in the same category. It differs as regards completeness of folds, and differs from the three other forms in having nearly twice the number of secondaries.

The specimen is relatively thick-bodied. It is a female, there being about 30 eggs in each ovary, which at least partly accounts for the width of the body.

* Named in honor of Mr. J. E. Guy Lionnet of the Department of Agriculture, Seychelles.

FIG. 4. *Hypogeophis rostratus lionneti* subsp. nov. Type. Nairobi National Museum (Coryndon Museum), No. A-602. Nairobi, Kenya, Africa. Total length, 252 mm.

Diagnosis. A medium sized form, the known length 250 mm; primary folds, 103; secondary, 48. Scales begin about the 20th fold. Two scale rows in a fold at middle of body; 4-5 rows in folds of posterior areas. Splenial teeth, 3-3.

Description. A relatively short plump caecilian. Head nearly triangular. The eye in a socket, forming a slight elevation externally; snout projecting beyond mouth 1.85 mm; tentacular aperture to eye, 2.9 mm, to nostril, 1.2 mm; eye to eye, 4.5 mm. Nostrils not visible from directly above head.

The two collars complete except second fused with first primary ventrally for a short distance; each collar with a transverse groove dorsally.

Primary folds, 102 about body; secondaries, 48, 6 complete. A few scales begin at about 20th fold dorsally. At the middle there are two continuous rows. Posteriorly there are 4-5 scale rows in each fold, the grooves relatively shallow and scales variable in size. The 11 first folds are complete as are the last 6-7. Those in between narrowly incomplete for most part.

Dentition. Premaxillary-maxillary tooth series, 20-1-20; prevomeropalatine, 21-1-22, of which 7-1-7 are prevomerine; dentary, 15-15; splenial, 3-3. The splenials relatively large on nearly same level as dentary teeth. Palate domed. The choanae separated by a distance equal to 2.2 times the diameter of one choana; the tongue has two well-developed narial plugs. The vomeropalatine teeth pass very close to choanae. The circular vent area relatively large, the denticles surrounding it much elongated and subequal. The terminus with a small unsegmented "shield."

Color. Lavender to violet with a distinctly lighter ventral shade; head grayish, growing lavender on occiput. Jaws and chin a very light shade of lavender. A cream spot at vent and slightly lighter areas about eye, nostril, and tentacle.

Measurements in mm. Total length, 252; head width, 7.7; body width at middle, 12.5; snout tip to first groove, 7.8; to second, 10; to third, 13.1. Width in length, about 20 times.

Remarks. The considerable increase in the number of secondaries (nearly double the number in the three known subspecies) indicates a fourth subspecies. Unfortunately no exact locality is known. The specimen has been on exhibition at the Coryndon Museum and bears only the label "Seychelles." No record could be found as to where or when it was acquired.

Key to Subspecies of *Hypogeophis rostratus* (Cuvier)

1. Secondaries less than 30 2
   Secondaries, 48; primaries, 102; reaching a known length of 252 mm. "Seychelles Islands" ..... *Hypogeophis rostratus lionneti* subsp. nov.
2. Fewer vertebrae (less than 105) 3
   More vertebrae (above 105, mean 109.3). Reaching a known length of 295 mm; primaries, 99-104; secondaries, 5-26. (No free-living aquatic stage.) Praslin and Curieuse Islands ..... *Hypogeophis rostratus praslini*

3. Range of vertebrae, 97-102 (mean 100.2). Reaching a length of 270 mm; secondaries, 17. Practically all primary folds complete. Frigate Island ..... *Hypogeophis rostratus guentheri*
Range of vertebrae, 100-107 (mean 104.9); primaries, 96-100; mostly complete; secondaries, 4-20. Reaching a known length of 365 mm. Mahé and Silhouette Islands ..... *Hypogeophis rostratus rostratus*

Ichthyophis taprobanicensis sp. nov.

(Figs. 5-6)

TYPE. American Museum of Natural History, No. 64515, Ohiya Area, Ceylon, 5500 ft. elev. PARATYPES. Naturhistorischen Museum Wien, No. 9109, Ceylon; American Museum of Natural History, No. 64541, Ceylon.

DIAGNOSIS. A short-tailed species, the longest specimen known, 260 mm; tail length in total length, 37-48 times; width in length, 22-24 times. Total body folds, 291-296, 8-10 confined to tail, ventrally angled anteriorly. Vent longitudinal. Scales begin on collars with 5-7 rows throughout most of body; splenial teeth, 10-10, to 12-12; no lateral light stripe.

DESCRIPTION OF TYPE. Head somewhat acuminate; eyes small and distinct; the distance between eyes, 5.2 mm; the distance from anterior eye level to snout tip, 4.9 mm; aperture of tentacle 1.7 mm from edge of eye; from nostril, 3.2 mm. Aperture of tentacle in an oval depression partly surrounded by a groove and a vague ridge reaching very close to lip edge. Nostril longer than wide, directed upwards, plainly visible from a point directly above head. Occipital region somewhat elevated.

First and second collars distinctly marked below and on sides but fused dorsally; second collar has two dorsal folds and on ventral surface fused to first primary for a short distance. Following the collars there are 291 folds (dorsal count), 284 folds (ventral count). Vent is longitudinal, with 7 denticulations on each side, interrupting three caudal folds. There are 8 caudal folds confined to tail. The latter compressed, ending in a blunt point. Terminal "shield" very small (1.5 mm long).

Folds are complete above and below, except for a few immediately following second collar, and they form a distinct angle throughout most of body along mid-ventral line. Preceding the vent, folds cross venter in straight line, and the ventral grooves, dim or absent on much of ventral surface, here are distinct.

Scales begin at second collar, there being 2 or 3 rows present at least dorsally. At middle of body the number of rows is 5 and in most of latter half of body 7 or 8 rows are present, the scales moderately large. Total number of scale rows on body dorsally estimated at about 1500.

Dentition. Four series of teeth present: premaxillary-maxillary series, 21-1-22, premaxillaries smaller than maxillaries; prevomeropalatine, 20-1-21, prevomerine teeth larger than premaxillaries, and bent nearly straight back or

FIG. 3. *Ichthyophis zapodamaensis* sp. nov. Type. American Museum of Natural History, No. 61815. Ceylon (5500 ft. elevation). Actual length, 260 mm. Dorsal, ventral, and lateral views of head; dorsal and ventral views of the terminus of body.

FIG. 6. *Ichthyophis taprobanicensis* sp. nov. Type. Ventral section of body, from near middle, showing the angled body folds. Actual body width, 11 mm.

mesially; dentaries, 19-20, the posterior teeth reduced in size; splenial teeth, 11-12. Choanae elongate, bordered on inner edge with slight angular ridge, the greatest transverse diameter of a choana is contained in distance between choanae about 4.5 times.

Color. Dorsally and laterally grayish lavender. Venter several shades lighter, this color appearing on sides; an area about vent and tip of snout whitish.

Measurements in mm. Total length, 260; tail length, 7; body width, 11; head width, 10; snout tip to first nuchal groove, 11; to second groove, 14; to third groove, 17.2 (measured laterally). Body width in length, 23.6 times; tail length in total length, 37 times.

REMARKS. *Ichthyophis orthoplicatus* has been described from Ceylon. This species differs from *taprobanicensis* in lacking the angle on the ventral part of most folds. It is presumed that *I. orthoplicatus* is a lowland form.

Ichthyophis laosensis sp. nov.

(Figs. 7-9)

TYPE. Museum National d'Histoire Naturelle, Paris, No. 1928 * 95. Specimen from "Haut Laos."

DIAGNOSIS. Specimen without lateral stripe, almost uniformly fawn colored with very little color difference between dorsum and venter. Eye in a socket not continuous with tentacular aperture. Collars not distinct above, the second with two posterior folds. Transverse folds, 346 (dorsal count), 345 (ventral count). Tail extremely short with only 5 folds, 2 interrupted by vent.

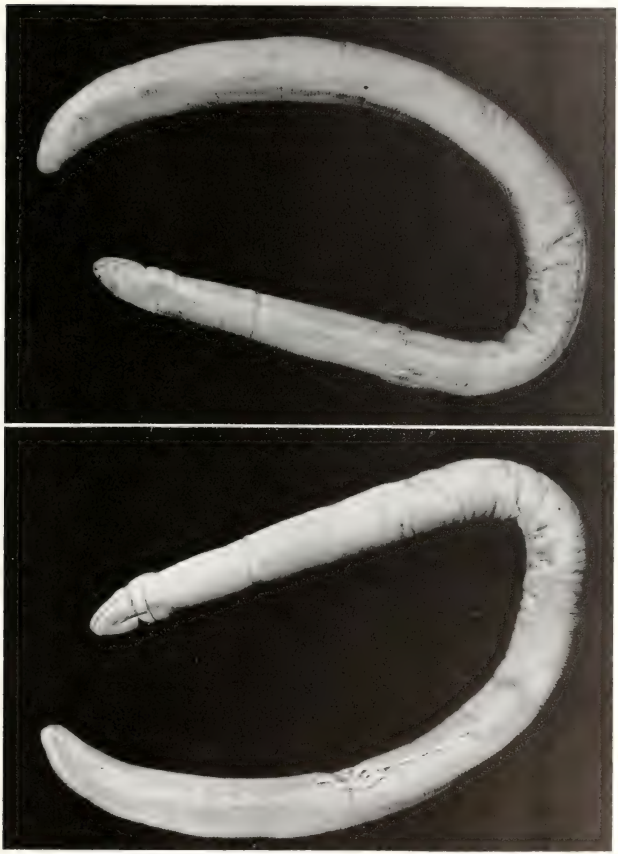

FIG. 7. *Ichthyophis laosensis* sp. nov. Type. Museum National d'Histoire Naturelle, Paris, No. 1928 * 95. From "Haut Laos," Asia. Total length, 318 mm.

Scales present, beginning on collars; posteriorly, three rows in each fold. Splenial teeth 16-16.

DESCRIPTION OF TYPE. Head moderate, not quite as wide as collars, eye very distinct; tentacle 1.6 mm from eye, 4.2 mm from nostril which is barely visible from directly above head; distance between eyes, 6.2 mm; from anterior eye level to tip of snout, 5.1 mm; snout tip to mouth angle, 9.5 mm.

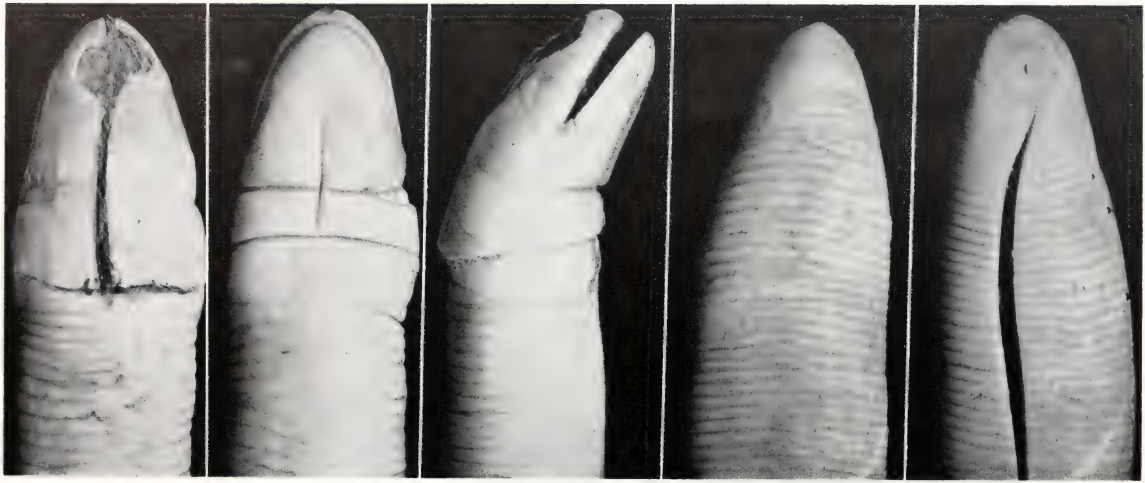

FIG. 8. *Ichthyophis laosensis* sp. nov. Type. Dorsal, ventral and lateral views of head; dorsal and ventral views of body terminus. Head width, 12 mm.

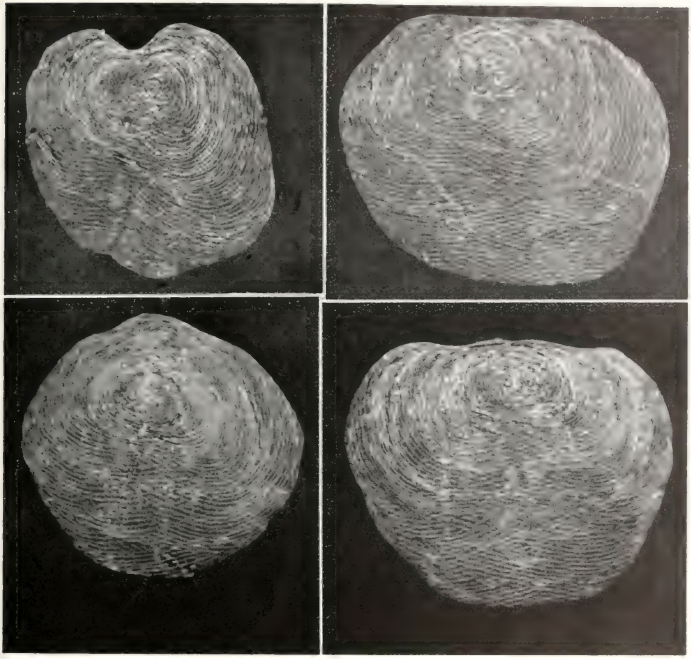

FIG. 9. *Ichthyophis laosensis* sp. nov. Type. Scales from the posterior part of the body: left, ventral; right, dorsal. Largest scale measures 2.0 × 1.5 mm.

Two collars following the occiput. First nuchal groove encircles neck, the second, while well developed ventrally, does not cross neck above; the two collars fused together above. Third nuchal groove is more or less visible above, but does not cross throat; the second collar, fused to first primary fold, bears two transverse folds on its posterior dorsal part.

Following the collars there are 346 transverse folds or annuli (dorsal count) and 345 folds (ventral count). Grooves separating folds are complete above but ventrally do not cross venter except posteriorly. However, if venter is examined under a lens, the folds themselves are complete and form a backward-pointing angle except in posterior part preceding vent where grooves and folds pass straight across venter. Tail extremely short, the vent small, longitudinal, with 6-7 fleshy denticulations on each side. Tail with 5 folds, 2 interrupted by vent. Total tail length from front of vent, 4 mm. Scales begin

on collars and at middle of body there are 2 irregular rows in each fold, increasing to 3 in posterior part of body.

Dentition. Four dental series. Premaxillary-maxillary teeth, 21-1-21, all about same size; prevomeropalatine series, 21-1-22, prevomerine teeth longer and curved back more than palatines; dentary teeth, 20-20, these slightly larger than maxillaries; splenials, 16-16, equally as large as prevomerine teeth. Tongue narrowed much anteriorly; choanae elongate, vaguely angulate, bordered posteriorly by narrow ridge separating choanal cavity from large palatal opening (filled with muscle) just behind it.

Color. Uniform fawn or clay-color, both above and below; no apparent whitish marks at eye, tentacle, nostril or vent. No evidence of lateral stripe.

Measurements in mm. Total length, 318; tail length, 4; width of head, 12; width of body, 13; snout tip to 1st groove, 12, to 2nd groove, 16.5, to 3rd groove, 22. Width of body in total length, 24.4 times; tail length in total length, 79.5 times.

Variation. Only the type is known. It may be related to *Ichthyophis acuminatus* but the head seems to be shaped differently and the dentition is reduced in all of the series. The color is essentially different.

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A New Family of African Gymnophiona[1]

EDWARD H. TAYLOR[2]

In a recent publication (Taylor, 1968), I presented a taxonomic revision of the order Gymnophiona, there recognizing three families. At the same time I suggested that there was a strong possibility that a fourth family should be recognized to include *Scolecomorphus*, an African genus comprising six known species. This opinion was based on preserved alcoholic material and in part on the literature dealing with the genus. However, at that time I had not personally examined a skull of a single species of the genus. The unusual anatomy of the skull had been studied by C. G. S. de Villiers (1938), who reported on some of the cranial features. In 1956, D. J. Brand made a second exhaustive study of the cranial anatomy of *Scolecomorphus uluguruensis* and compared it to skulls of other caecilian genera. Neither author was concerned primarily with taxonomy.

In my recent anatomical studies I have had available the skulls of two species of this genus—*Scolecomorphus vittatus* and *S. kirkii*. These have confirmed my belief that it is imperative to recognize the family Scolecomorphidae as a fourth family of the Gymnophiona, and it is here described.

Family Scolecomorphidae fam. nov.

(Figs. 1-5)

The type genus of the Scolecomorphidae is *Scolecomorphus* Boulenger (1883), a genus with six recognized species, all African in distribution, being known in Kenya, Tanzania, Malawi, Zambia and the "Cameroons."

The general characteristics are: primaries, so far as known, 120-154; no secondary folds; a terminal unsegmented "shield"; no scales present; splenial teeth absent; eyes degenerate, under bone, without orbit (or drawn forward into tentacular open groove by tentacle); tentacle with an external subglobular swelling, partly surrounded by a groove, through which the extrusible part of tentacle is extended; male penis bears numerous spines of variable

[1] This work was pursued under a National Science Foundation Grant, No. GB-4101.
[2] Research Associate, University of Kansas Museum of Natural History.

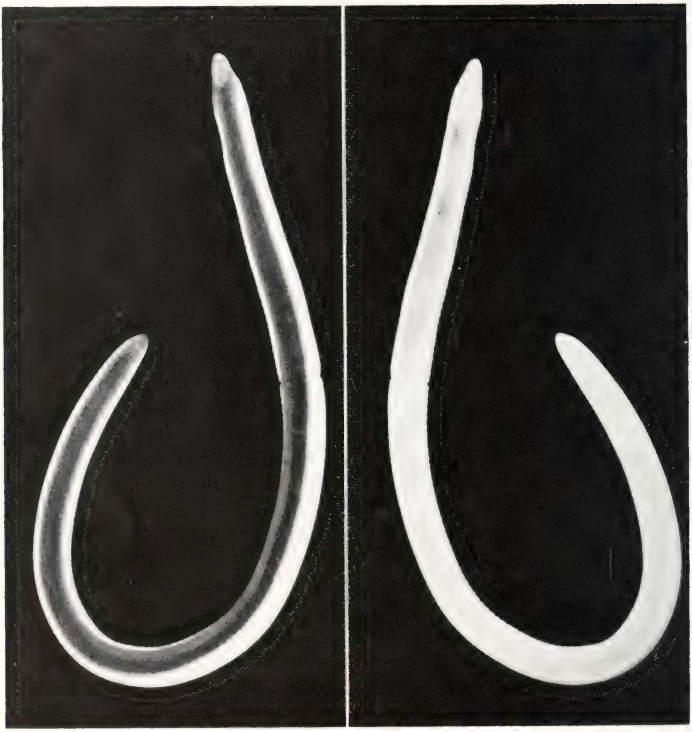

FIG. 1. *Scolecomorphus vittatus* Boulenger. National Mus. Nairobi, No. A-142. From Amani, East Usumbara Mountains, Kenya, Africa. Dorsal and ventral views. Actual length, 163 mm.

size which may or may not be arranged symmetrically; strong diastema present between prevomerine and palatine teeth, the latter being directed outward diagonally rather than posteriorly; no narial plugs on tongue; seemingly no group loss or group replacement of teeth.

The cranial characters readily visible in a prepared skull are: dorsal surface from front to back roofed, in order named, with paired elongate nasals, paired frontals lengthened on sides, and a pair of parietals which reach almost to foramen magnum. This foramen surrounded by posterior part of compound basisphenoid which is sutured behind the parietals.

Lateral to this median area and bordering the median roof are first the septomaxillae, partly bordering the nostrils, the maxillopalatine and the squa-

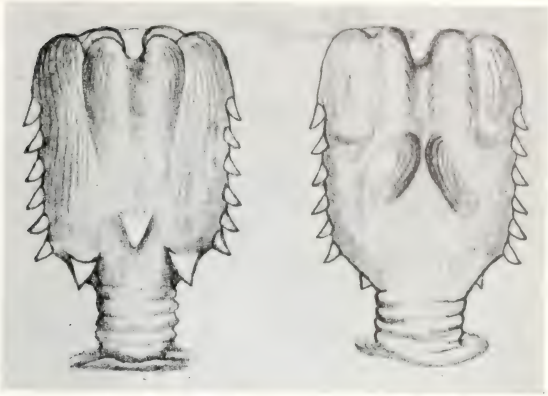

Fig. 2. *Scolecomorphus uluguruensis* Barbour and Loveridge (From Taylor, 1968, p. 655, fig. 361). Dorsal and ventral views of the extended penis showing spines. Much enlarged.

mosals, these latter bones widely separated from parietals and posterior part of frontals by extremely large diastemata that leave much of lateral surface of braincase visible from above. Palatine shelves and orbitosphenoids surround internal nares. Otic capsules somewhat inflated as seen from above. No eye socket present, the eye covered by bone (or in this case the eye pulled by the tentacle forward into open tentacular groove and lying beside edge of septomaxilla below nostril.

Tentacular aperture in skull begins near middle of maxillopalatine, widening anteriorly. It is visible from ventral surface of skull.

Snout extends some distance beyond premaxillary tooth row, this tooth series continuous with maxillary series, both much in advance of short prevomerine series. Palatine series on palatine shelf of maxillary separated from provomerine teeth by wide diastema, the series directed diagonally outward and coming to lie directly behind maxillary series, yet not continuous with it. Prevomerine bones are narrowed, in contact with each other for more than four-fifths of their length, the portion anterior to prevomerine teeth longer than the part posterior to them. A wide diastema between basisphenoid (with the orbitosphenoid) and squamosal, thus exposing much of surface of orbitosphenoid as well as the posterior sides of the braincase.

Quadrates are sutured to posterior ends of squamosals. Stapes are completely absent (or perhaps completely incorporated into the compound bone here called the basisphenoid).

In one skull an area on maxillary superficially appears to be a prefrontal, but this solidly fused to maxillary. However, septomaxillae are definitely separate bones reaching below nostrils to contact small premaxillae.

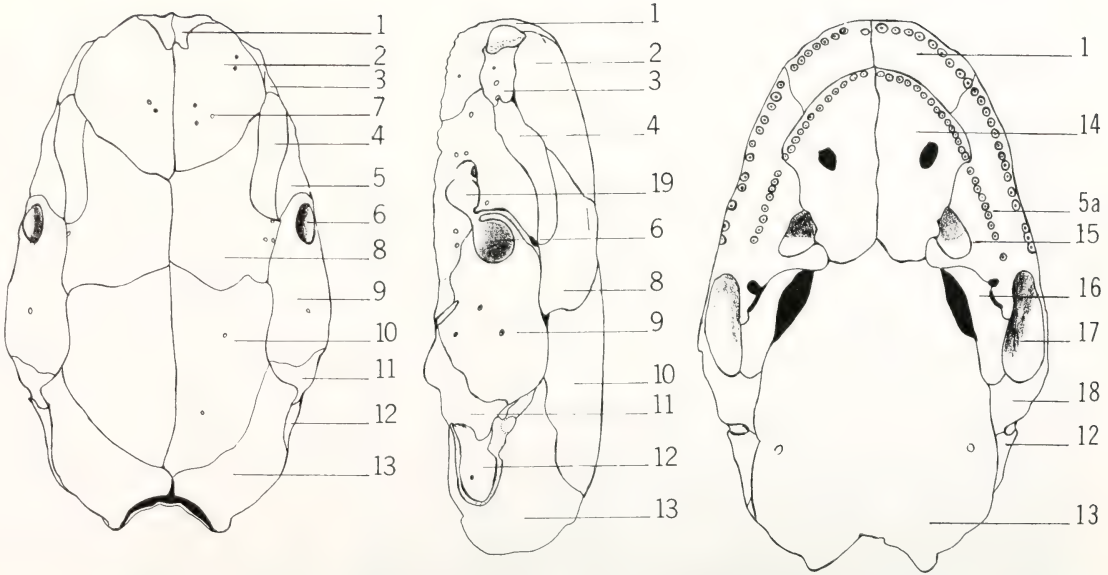

Fig. 3. Diagrams of a typical skull of Gymnophiona. Dorsal, lateral, and ventral views of the skull of *Caudacaecilia weberi* (Taylor). 1, premaxillary; 2, nasal; 3, septomaxilla; 4, prefrontal; 5, maxillary; 5a, palatine shelf of maxillary; 6, orbit of eye; 7, fenestra for nerves and blood-vessels; 8, frontal; 9, squamosal; 10, parietal; 11, quadrate; 12, stapes; 13, basisphenoid (compound); 14, prevomer; 15, internal naris (choana); 16, pterygoid; 17, fenestra for jaw muscles; 18, quadrate; 19, tentacular groove.

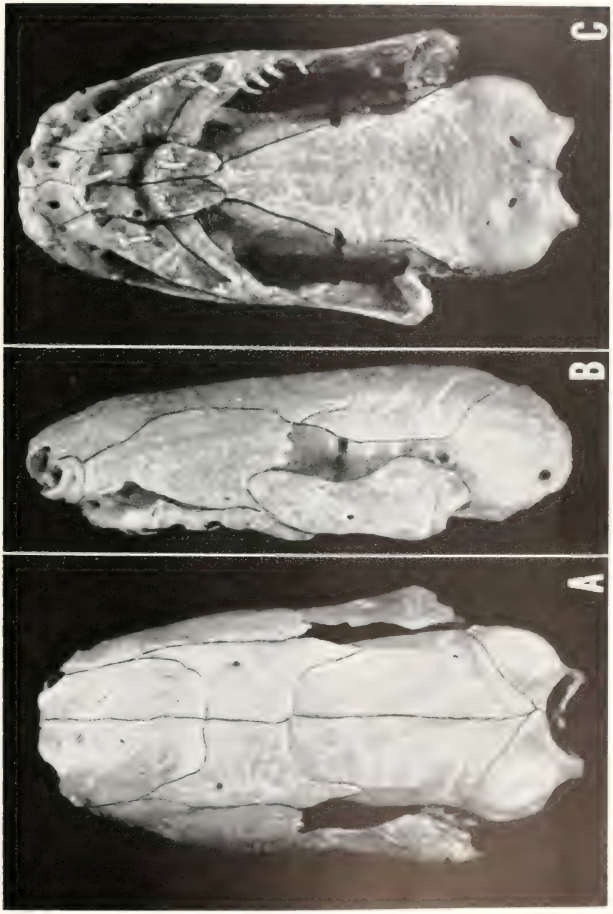

Fig. 4. *Scolecomorphus kirkii* Boulenger. Museum of Comparative Zoology, Harvard College, No. 27120, Cholo Mountains, Cholo District, Nyasaland (Malawi), Africa. Dorsal, lateral and ventral views of the skull. Actual skull length, 7.5 mm.; greatest width, 1.05 mm.

The bones of the skulls of the species in this genus seem extremely fragile and certain bones poorly attached. (For more minute details of the skull structure, consult the excellent papers of C. G. S. de Villiers (1938) and D. G. Brand (1956).)

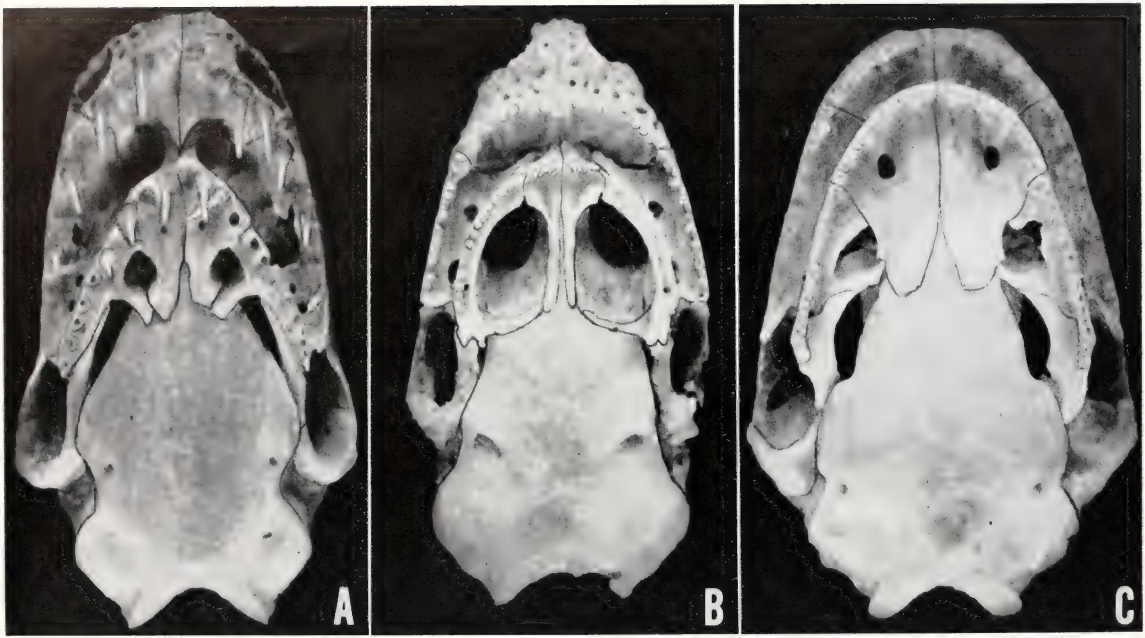

FIG. 5. Ventral views of three skulls. A. *Caecilia degenerata* Dunn. American Museum of Natural History, No. 23554. Actual length of skull, 10.1 mm; greatest width, 5.8 mm. Representative Caeciliidae. B. *Potamotyphlus kaupii* (Berthold). University of Illinois Museum of Natural History, No. 787. Actual length of skull, 10.9 mm; greatest width, 5.7 mm. Typhlonectidae. C. *Caudacaecilia asplenia* Taylor. American Museum of Natural History, No. 23354. Actual skull length, 9.8 mm; greatest width, 6 mm. Ichthyophidae.

As in all gymnophiones, the lower jaws articulate with the quadrate. Each side of the jaws is composed of two compound bones, the dentary, which bears the dentary teeth, and the articulare. Splenial teeth are not present.

For purposes of comparison, I include here a plate (Fig. 5) showing photographs of skulls representative of the three other recognized families—Caeciliidae, Typhlonectidae, and Ichthyophidae. While neither the skulls nor the photographs are perfect, anyone more or less familiar with the vertebrate skull may follow the comparisons given for this face of the skull.

Fig. 5A is a photograph of the skull of *Caecilia degenerata* which is fairly typical of the genus *Caecilia*, perhaps less so of the entire family of the Caeciliidae. In this skull the prefrontals, oculars and septomaxillae are absent as separate bones. The nasals and the premaxillae are fused to form the nasomaxillae. The frontals are completely separated by the mesethmoid (a character that is not universal in the Caeciliidae [in the sense here understood]).

Compare the *Scolecomorphus* skull with this as regards the position and arrangement of the prevomerine teeth and the shape and character of the prevomers themselves. Compare the broadly exposed expanse of the orbitosphenoid, observing its condition in *Caecilia*. Note the broad diastemata in the continuity of the prevomerine teeth and palatine teeth and the lack of diastemata in *Caecilia*.

Fig. 5B is a representative of the aquatic family, the Typhlonectidae. The skull is that of *Potamotyphlus kaupii* (Berthold). Observe that the internal nares are relatively enormous and that the diastemata between the prevomerine and the palatine teeth are small. There is no broad exposure of the orbitosphenoid since the fossa between the basisphenoid and pterygoid, and the maxillopalatine, is practically nonexistent. The dorsal conformation of the skull shows the absence of the prefrontals, the septomaxillae and the oculars, while the premaxillae and the nasals are fused to form the nasopremaxillae. Dorsally a broad diastema is present between the parietal and squamosal. The orbit of the eye is cut between the squamosal and the maxillopalatine. The tentacular aperture emerges from the anterior end of the maxillopalatine. The stapes is present, the nostril very large.

Fig. 5C is a representative of the Ichthyophidae. The prevomers are greatly widened. The dental series are subparallel. The pterygoids are flattened, not fused with the quadrate. The stapes is present, making contact with the quadrate. The skull on the dorsal and lateral surfaces has the separate premaxillae, nasals, prefrontals, septomaxillae, and oculars.

The genera of the Caeciliidae, as that family is now composed without the three other recognized families, seem to fall into two groups which differ very considerably and consistently. I consider these of subfamily rank and consequently propose two subfamilies, the Caeciliinae and the Dermophiinae.

In the Caeciliinae I include the genera *Caecilia* Linnaeus and *Oscaecilia* Taylor, the subfamily characters being the generic character of these two forms. The group is confined to South America.

In the Dermophinae I place the somewhat heterogeneous genera, as widely distributed as the order *Gymnophiona,* as follows: *Cryptopsophis* Boulenger, *Gymnopis* Peters, *Dermophis* Peters, *Boulengerula* Tornier, *Gegeneophis* Peters, *Microcaecilia* Taylor, *Geotrypetes* Peters, *Grandisonia* Taylor, *Idiocranium* Parker, *Brasilotyphlus* Taylor, *Herpele* Peters, *Siphonops* Wagler, *Mimosiphonops* Taylor, *Praslinia* Boulenger, *Luetkenotyphlus* Taylor, *Parvicaecilia* Taylor, *Afrocaecilia* Taylor, *Uraeotyphlus* Peters, *Pseudosiphonops* Taylor, *Copeotyphlinus* Taylor, *Schistometopum* Parker, *Indotyphlus* Taylor, and *Hypogeophis* Peters. Whether the Dermophinae actually comprise all these genera cannot be determined with certainty until more is known of the anatomy and life histories of many of the genera.

KEY TO THE HIGHER GROUPS OF THE GYMNOPHIONA

1. Three pairs of *branched gills* arise laterally from pharynx with one or two functional gill slits, the gills usually absorbed before birth or hatching; gill slits function in those that are semiaquatic after hatching; organism may be semiaquatic during entire larval stage. Oviparous or ovoviviparous 2
   Larval gills arise from a dorsal point immediately following the occiput. These are *baglike, very close together* (may be connected at the base) *and are absorbed before birth.* Entirely aquatic, viviparous (ovoviviparous). External nares large, internal nares very large. Skull bones reduced in number, the premaxillae and nasals fused to make the two nasopremaxillae. Prefrontals, oculars, and septomaxillae absent. Stapes present, joining the quadrate; a large diastema between the parietal and squamosal. No scales; no secondary folds; no tail; eyes in sockets ..... Typhlonectidae
2. Septomaxillae, premaxillaries and nasals present as separate bones; stapes present or absent. Prefrontals and oculars present or absent 4
   Septomaxillae absent, the premaxillaries and nasals fused to form the nasopremaxillae; stapes present. Prefrontals and oculars absent ..... Caeciliidae 3
3. Premaxillary-maxillary teeth much enlarged, part of the series lost in groups and replaced in groups; part of prevomerine series and dentaries lost in groups and replaced in groups; eye in socket or bone covered; scales present or absent, secondaries present or absent; the number of vertebrae for the most part greater than in other genera. Life history practically unknown; scales present or absent. South and Central American ..... Caeciliinae
   Premaxillary-maxillary, dentary, and prevomerine teeth presumably not lost or replaced in groups. (Eye in socket or bone covered?) Teeth not especially enlarged proportionally ..... Dermophinae
4. Prefrontal and ocular bones present, the latter may be partly fused to squamosal. Stapes present. Orbitosphenoid not widely exposed on ventral surface of skull. Primaries for the most part divided into three or four secondaries. A tail is retained; eye well developed in a socket; vent (except *Rhinotrema*) longitudinal. No distinct diastema between prevomers and palatine teeth. Tentacle closer to eye than nostril; scales invariably present.

The tadpoles passing through an aquatic stage of varying duration but eventually terrestrial. No spines on penis; splenial teeth usually numerous ..... Ichthyophidae

No prefrontal or ocular bones. Orbitosphenoid clearly visible from ventral surface of skull. A diastema between the prevomerine and the palatine teeth, the latter directed behind the end of the premaxillary maxillary series. No stapes present. Spines on penis. No secondaries. No scales. No tail. Eye under bone (no socket). Tentacle close to nostril. Splenial teeth absent ..... Scolecomorphidae

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

VOL. XLVIII PAGES 307-313 MAY 16, 1969 NO. 11

A New Caecilian from Brasil[1]

EDWARD H. TAYLOR[2]

In reviewing the caecilians in the Institut für Spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin, I noted a small caecilian which I regard as new and belonging to the recently described genus *Microcaecilia* Taylor. With the kind permission of Dr. Günther Peters, the curator of the collection, I describe this as

Microcaecilia supernumeraria sp. nov.
(Figs. 1-4)

HOLOTYPE. Zoologisches Museum der Humboldt Universität, Berlin, No. 5268 from "São Paulo," Brasil, collected by "Haeckel." No paratypes.

DIAGNOSIS. A small caecilian reaching a known length of 258 mm; eye, covered solidly with bone, not usually visible externally; tentacular aperture considerably posterior to nostril in what would probably be a normal position of the eye in caecilians; first and second collars complete, each with a dorsal transverse groove. Primary folds 143; secondary folds, approximately 98; splenial teeth absent; maxillary teeth, 7-1-7. Scales relatively large, more or less visible externally under the edges of the folds. Scales begin near collars and form four or five rows in grooves of folds throughout much of body; subdermal scales relatively large, very numerous, widespread.

DESCRIPTION OF THE HOLOTYPE. When body is stretched (to eliminate sinuous curves of spine), specimen approximately 258 mm in length, the general width approximately 6.2 mm (posteriorly somewhat flattened and a little wider), width in length, approximately 41.6 times. Seen from above, head somewhat oval, narrow, short, relatively thick, the greatest width, 5 mm; the line of the mouth, seen laterally, strongly curving down anteriorly. Length of head from tip of snout to first nuchal groove, 6.2 mm; to the third nuchal groove (lateral measurement), 11 mm. Snout projects beyond mouth 1.2 mm.

[1] This work has been pursued under a National Science Foundation Grant, No. GB-4510.
[2] Research Associate, University of Kansas Museum of Natural History.

FIG. 1. *Microcaecilia supernumeraria* sp. nov. Zoologisches Museum der Humboldt-Universität, Berlin, No. 5268 from "São Paulo, Brasil". A. Ventral, B. Dorsal view. Total length of specimen, 258 mm.

Eye, if present, without socket and covered by bone. The tentacular aperture lateral, not or scarcely visible from directly above head, separated from nostril by a distance of 2 mm, its distance from edge of lip about 0.25 mm; nostrils far forward, not or barely visible from directly above head. Tip of snout rather rounded in lateral profile.

First collar distinctly delineated by two first nuchal grooves, both of which are distinct, surrounding neck. Short transverse groove on doral part of collar. Second collar likewise distinct save that it is fused for a short distance

Fig. 2. *Microcaecilia unipunctata* sp. nov. Type. A-C. Dorsal, lateral and ventral views of head. D. Ventral view of the mandibular region. Greatest width of head at first mental groove, 5 mm.

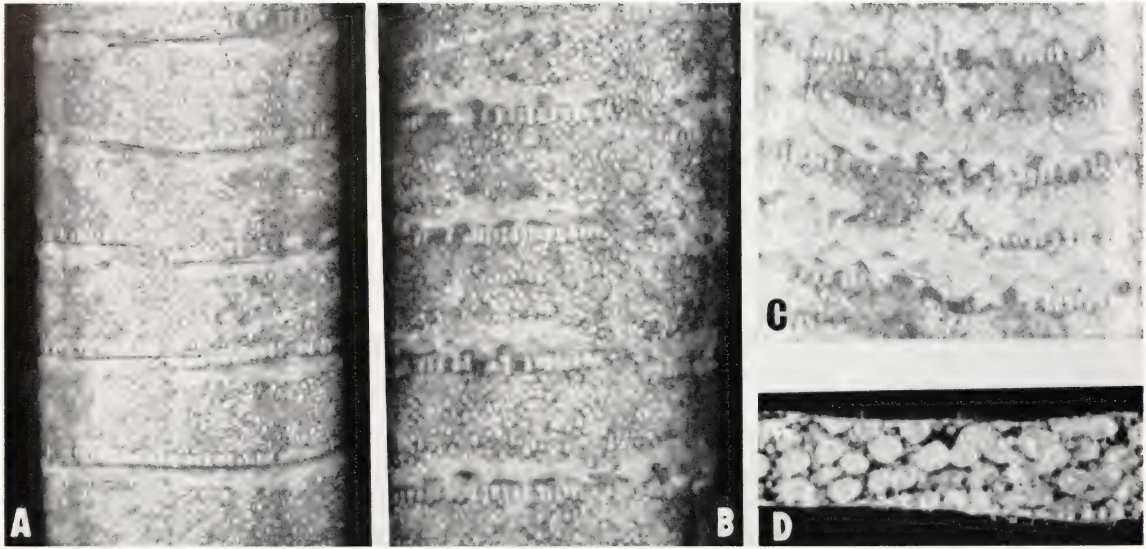

FIG. 3. *Microcaecilia supernumeraria* sp. nov. Type. Section of body near middle. B. Section of body posterior to middle. S. Section of body in last fifth showing scale rows visible externally. D. Section of connective tissue showing the subdermal scales in situ.

below with first primary fold; it bears a transverse groove dorsally. Following the collars are 143 primary folds, almost all completely surrounding the body; about 93 secondary folds, most of which completely surround body (slightly irregular posteriorly). No unsegmented terminal "shield," body terminus rather bluntly rounded seen from above, and flattened on its under surface. Vent transverse, the ends of terminal folds entering vent from behind. Denticulations at its edge not or scarcely discernible.

Scales begin at first primary fold. At first very small, transversely widened, the series however completely surrounding the body at fourth primary. At middle of body, scales a little larger, in four (or five) rows at least dorsally, but here nearly as large as in posterior folds; in last 2 centimeters of body, the scales usually in 4 imbricate rows in both primary and secondary grooves, the smallest scales forming uppermost row.

Aside from scales in the grooves, subdermal connective tissue scales present over much of body and these vaguely evident externally through epidermis when surface of body is dry. These relatively large, equalling those that may occur in much larger caecilian species.

While grooves have a row of elongate glandules arranged longitudinally which seemingly give rise to the scales in groove, subdermal scales seem to be produced from a glandule not greatly unlike the numerous glands of the epidermis and, like them, not incumbent.

Dentition. Teeth arranged in three series. Premaxillary maxillary teeth, 7-1-7, forming a relatively short series not extending back as far as level of choanae; prevomeropalatine, 14-1-13; dentary, 11-11; splenial, 0-0; the anterior dentary teeth largest, the palatine series smallest.

Choanae rather large, the transverse diameter of one in distance between them about 1.5 times; tongue rather pointed at tip, free, lacking narial plugs.

Measurements in mm. Total length, approximately 258; width of head, 5; width of body, 6.2; width in length about, 41.6 times.

Color. The type is seemingly faded, the anterior part of the body light brown, the remainder light fawn to whitish; top and lateral surfaces of head cream to ivory white, lower jaws lighter than chin.

Remarks. When the preservative evaporates from the surface of the body, the grooves show a distinct white line caused by the white color of the scales appearing through the epidermis, and the intervening areas may be clouded with whitish from the subdermal scales which may become more or less visible also.

This form differs from the three other species recognized in this genus in having 40 more secondaries and 20 more primaries. In addition, both the typical scales of the folds and of the connective tissue are very numerous and relatively large, more numerous and larger than in other known species of the genus.

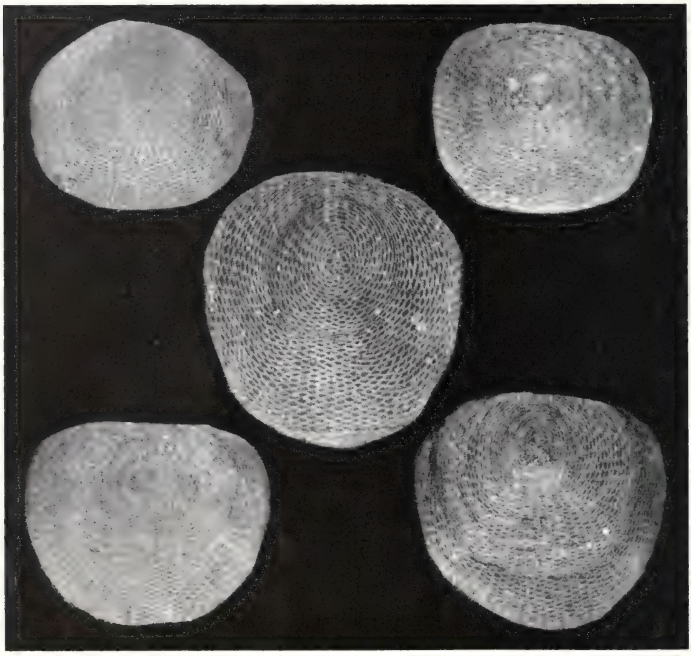

FIG. 4. Several large scales from *Microcaecilia supernumeraria* sp. nov., from posterior dorsal part of body. Largest scale about 1.0 × 1.35 mm.

Subdermal scales may be present in other genera of the Caeciliidae. I have found them only in the genera *Oscaecilia* and *Caecilia*. In *M. supernumeraria* these scales may attain a size of 0.3 to 0.35 mm; in *M. albiceps* they are usually smaller, 0.1 to 0.2 mm.

The genus *Microcaecilia* described by Taylor (1968, p. 532) (type species *Dermophis albiceps* Boulenger) is widespread in South America. Three species are known besides the one herein described. The oldest known form is *Microcaecilia unicolor* described by A. Duméril (1864) in the genus *Rhinatrema* (in his Fig. 7 it is called *concolor* by error). The type locality is Cayenne. Since that time it has been considered in the genus *Dermophis* or *Gymnopis*.

A second species, *Microcaecilia albiceps*, was described by Boulenger (1882, p. 98, pl. 8, fig. 1) in the genus *Dermophis*, the type being from Ecuador. Subsequently it has been treated in both *Dermophis* and *Gymnopis*.

More recently Roze and Solano (1963) described *Microcaecilia rabei* in the genus *Gymnopis* from Southwestern Venezuela.

These forms agree in the following generic characters: eye, if present, concealed under bone, lacking an eye socket; tentacular aperture far from nostril in about what would be a normal position for the eye in a caecilian. The line of the mouth seen laterally curves down; the number of premaxillary-maxillary teeth generally reduced, the series not extending back to level of internal nares. The splenial teeth are entirely absent. Scales are present in the primary and secondary grooves at least in much of body; many connective tissue scales may be present.

Microcaecilia albiceps is not uncommon in eastern Ecuador but probably does not occur in the Pacific drainage of that country. *M. rabei* is known only from the State of Bolívar in Venezuela. *M. unicolor* occurs in Cayenne. I have referred to it one specimen from Río Oko, British Guiana (Guyana) although it differed from the type in having the maxillary-premaxillary teeth 17-1-17. Material from this area should be acquired and carefully examined, as I may have erred in so disposing of this specimen. I was unable to demonstrate the presence of subdermal connective tissue scales in the specimen.

The following brief key may serve to distinguish the four forms:

Key to Species of *Microcaecilia* Taylor

1. Head whitish (cream, fawn, grayish white, or yellowish) usually nearly uniform. Body plate 2
   Head not so colored 3
2. Secondaries less than 70 (48-62); primaries, 115-123. Eastern Equador ..... *albiceps*
   Secondaries more than 70 (94); primaries, 143; São Paulo, Brasil ..... *supernumeraria*
3. Body generally some shade of lilac, violet, or lavender, the head of a lighter shade of the same color; secondaries, 21-34; primaries, 108-117; Southeastern Venezuela ..... *rabei*
   Body usually nearly uniform brown (possibly some shade of lilac or lavender in life); the head clouded with brownish; secondaries, 55-75; primaries, 98-118. French Guiana and British Guiana (Guyana) ..... *unicolor*

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THE UNIVERSITY OF KANSAS
SCIENCE BULLETIN

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A New Panamanian Caecilian[1]

EDWARD H. TAYLOR[2]

In the summer of 1966 I visited the Canal Zone and other parts of Panamá with the intention of exploring for caecilians. Mr. Charles Myers, then of Gorgas Memorial Laboratory, provided me with transportation and accompanied me to the ancient volcano now called El Valle de Antón, in the crater of which is the village of Antón, in the province of Coclé.

Caecilians were discovered here in a small swampy area not far from our hotel. In order that this form may be distinguished easily from the other caecilians of Panamá, I append a short key to follow the description.

I desire to acknowledge my indebtedness to Mr. Myers for his very considerable help and numerous courtesies.

Caecilia volcani[3] sp. nov.

(Figs. 1-4)

HOLOTYPE. Edward H. Taylor - Hobart M. Smith (EHT-HMS) Coll. No. 4689 ♂. Collected at El Valle de Antón, Coclé, Panamá (elev. 550m) by Edward H. Taylor and Charles Myers, July 11, 1966. Topotypic paratypes 4690-4697, same date and collectors.

DIAGNOSIS. A medium small swamp-dwelling caecilian reaching a known length of 324 mm; tip of snout truncate; eyes visible externally, slightly raised, in a socket; tentacle emerges below and slightly in advance of nostril, not visible from above, closer to mouth than to nostril; primary folds, 112-124; secondary folds, 14-32. Primaries complete dorsally only on the first three centimeters following collars, and in last two centimeters preceding the terminus. Folds incomplete below except on last two centimeters. The terminus transversely pinched (flattened). Premaxillary and prevomerine tooth series with group loss and replacement. Tongue with narial plugs; splenial teeth present.

[1] This work was pursued under a National Science Foundation Grant, No. GB-4510.
[2] Research Associate, University of Kansas Museum of Natural History.
[3] Named for Volcanus, god of fire.

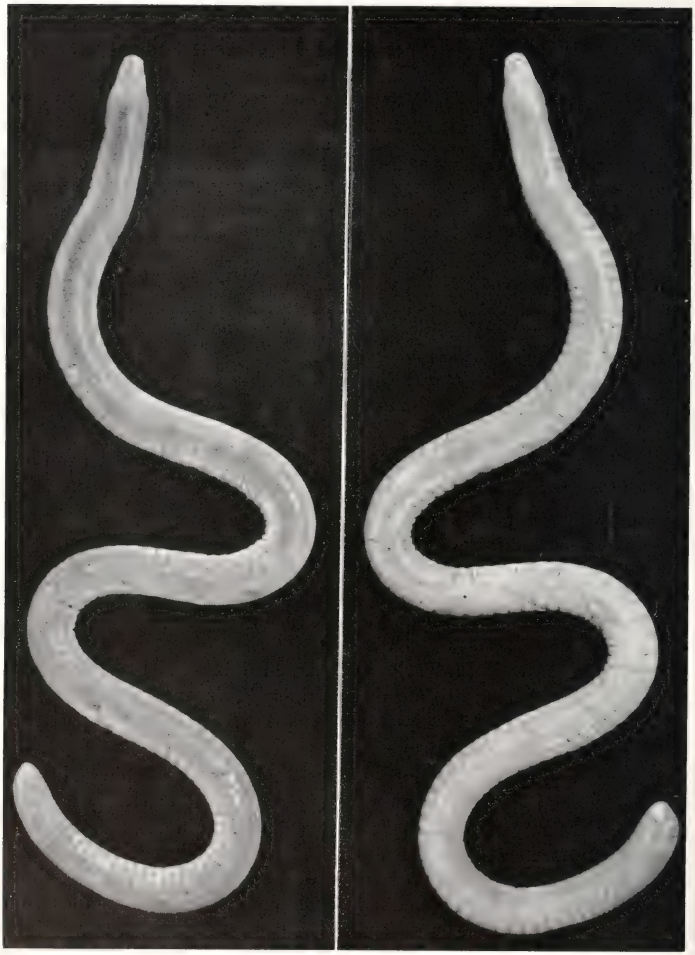

FIG. 1. *Caecilia volcani* sp nov. EHT-HMS Coll., No. 4689 ♂. Type. Dorsal and ventral view. Actual length of specimen, 320 mm. El Valle de Antón, Coclé, Panamá.

DESCRIPTION OF THE HOLOTYPE. The total length 320 mm, the body width in length 30.5 times. Head somewhat truncate, the nostrils well visible from above, the greatest width of head at first nuchal groove, 7.6 mm, while width

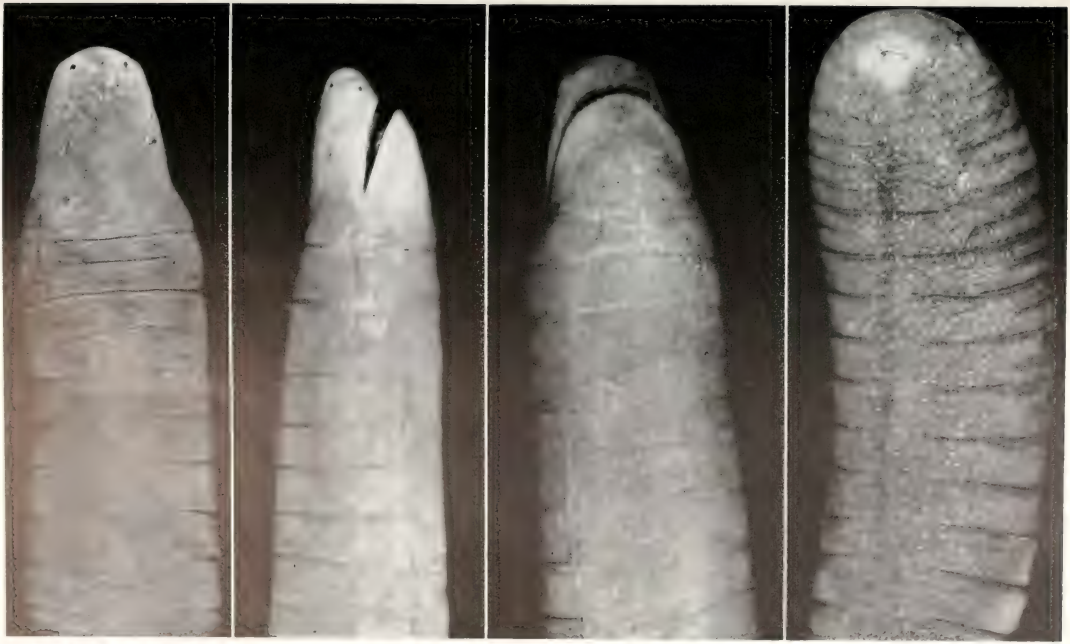

Fig. 2. *Gymnopis multiplicata* sp. nov. Type. Dorsal, lateral and ventral views of head and neck; ventral view of subcaudal area. Head width at first annulus 7.6 mm.

at nostrils is 5.2 mm; tentacular aperture below and slightly in advance of nostril. Eye distinctly visible, in a socket, the distance from the tentacular aperture, 3.6 mm; tentacle to nostril, 1.4 mm; eye to nostril, 3.7 mm.

First nuchal collar delineated by the first nuchal grooves, clearly defined below, less distinct dorsally; a short dorsal transverse groove on collar. Second collar defined by the second and third nuchal grooves, but third groove broken below permitting a fusion of second collar with first primary fold. Second collar much wider than first. Following the collars are 124 primary folds, 32 secondary folds (counting from first appearance, even though an occasional one may be missing). There are three complete or almost complete secondaries.

Vent transverse with about seven irregular denticulations preceding and a similar number following vent. Two of the anterior denticles bear small rounded moundlike anal glands; distance of vent from body terminus, 2 mm; width of body one-half cm from terminus, 9.6 mm.

Dentition. Premaxillary-maxillary tooth series, 12-1-12, three alternating teeth on each side of premaxillaries missing but being replaced by teeth developing in the gums; prevomeropalatine series, 9-1-9, with three alternating teeth on each side of middle being replaced. Dentary teeth, 10-10, the anterior the largest in mouth, while posterior dentaries are minute; splenial teeth, 2-2, small. The tongue has two well-defined narial plugs, area between them and area behind them striate longitudinally. Choanae subcircular, the diameter of one, in distance separating the two, about two times.

Scales. These begin in the folds near middle of body; a few at first, then a single row of scales. Near terminus, scales distinctly larger, subquadrangular, overlapping toward middorsal scale (about 18 large scales in one fold); those on ventral parts somewhat smaller than dorsals. These scales in thin tissue pockets. Laterally on body, even anterior to the scales in folds, there may be small scales in connective tissues beneath skin. These are nearly circular, the largest being about 0.3 mm in diameter (see Figs.).

Color. Uniformly slate, vaguely grayer on head and neck; underside of snout and edges of lips lighter gray. A vague light spot about eye, one in front of nostril and one at aperture of tentacle. Ventral surface of body grayish slate, somewhat darker in median ventral region. Narial plugs on tongue dark, nearly black.

Measurements in mm. Total length, 320; head width, 7.6; body width, 10.5; width in length, about 30.5 times; snout tip to first groove (lateral), 8.6; to second groove, 12.4; to third groove, 17.

Skull characters (from a paratype). Skull characteristics from the cranium of EHT-HMS, No. 4696, topotypic paratype. The skull roofed by a nasopremaxillae, frontals and parietals, together with a median mesethmoid which completely separates frontals and pushes between posterior parts of naso-

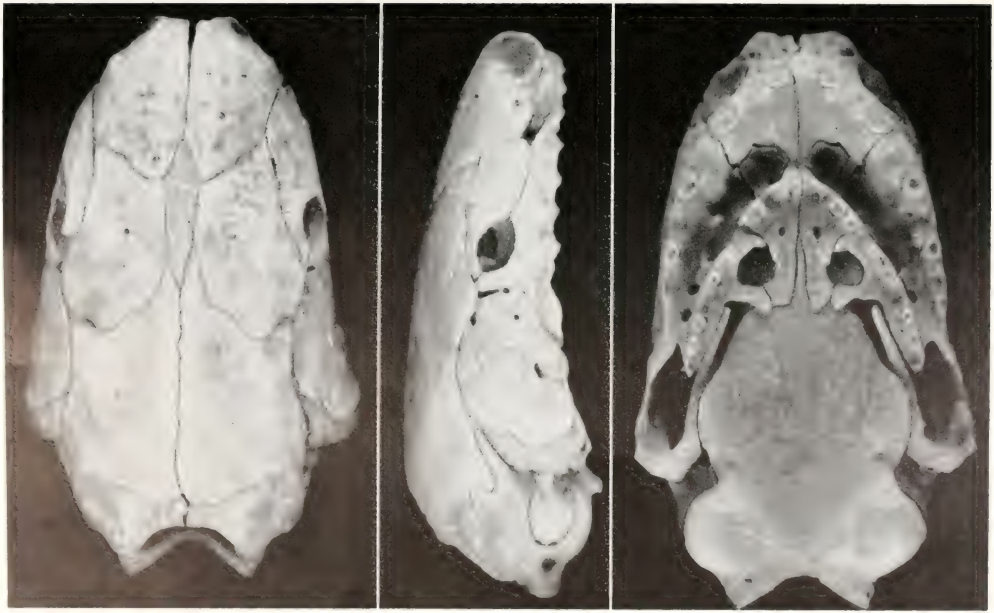

Fig. 3. *Caecilia volcani* sp. nov. EHT-HMS Coll., No. 4096.5, topotypic paratype. Dorsal, lateral and ventral views of skull. Actual skull length, 8.5 mm; greatest width, 5.1 mm.

premaxillae and anterior parts of parietals. Foramen magnum surrounded by a compound bone, the basisphenoid, sutured between parietals and the foramen.

Lateral to these bones are, in sequence, the maxillopalatines, squamosals, and quadrates. The stapes, which lie against the basisphenoidal wall of posterior part of brain case and against otic capsules, attach to quadrate. The otic capsules are inflated. There is a fine suture running from orbit of the eye to tentacular aperture which seems to separate off a prefrontal, but both the part above suture and that below seems to be solidly a part of maxillopalatine. I have not noted this condition in skulls of other species of *Caecilia* that I have examined.

Ventral surface shows two nasopremaxillae extending back from premaxillary teeth almost reaching prevomerine teeth. Immediately behind these are two rather reduced prevomers with two irregular processes anterior to prevomerine teeth, and pushing back between and bordering the inner sides of the internal nares. Remainder of the nares bordered by palatal shelves of maxillopalatines. Pterygoid extends forward along palatine shelf but is separated from basisphenoid by narrow diastema. Basisphenoid has an elongate spine forward separating prevomers for more than half their length. It widens where in contact with the pterygoid and quadrate, behind which is a constriction.

Measurements, in mm, of the skull and the tooth counts are given herewith: Total length, 8.5; greatest width, 5.1; width of skull at orbit, 4.15; jaw length, 7.0; total length of basisphenoid, 5.6; width at wings, 3.4; width behind constriction at otic capsules, 3.5; length of prevomers, 2.5; their combined width, greatest, 1.9; premaxillary teeth, 4-3; maxillary teeth, 6-6; prevomerine teeth, 3-3; palatine teeth, 5-5; dentary, 11-11; splenial, 1-1.

Remarks. El Valle de Antón is an ancient volcanic crater. The village occupies the basin, which is relatively flat. In the eastern part of the town a small stream drains from the higher hills to the north. Along this narrow valley is a road. At one point a small swamp drains into the stream, the water dribbling down the relatively low bank. The swamp was covered with a heavy growth of a giant grass resembling wild sugar cane. The specimens of caecilians were dug out of the soft mud bank. Some individuals fell into the water and escaped.

The relationship of the species may presumably be with *C. degenerata* and *C. orientalis*. One of the significant differences is the presence of well-developed secondaries and the general characteristics of the squamation. Subdermals have not been demonstrated in the two other species mentioned, and scales in folds may be absent or a few may occasionally be present. Seemingly the relationship with the *Caecilia tentaculata* and *C. nigricans* occurring also in Panamá (Darién) is distant. I regard the Panamanian *ochrocephala* formerly associated with *Caecilia*, as a member of the genus *Oscaecilia*.

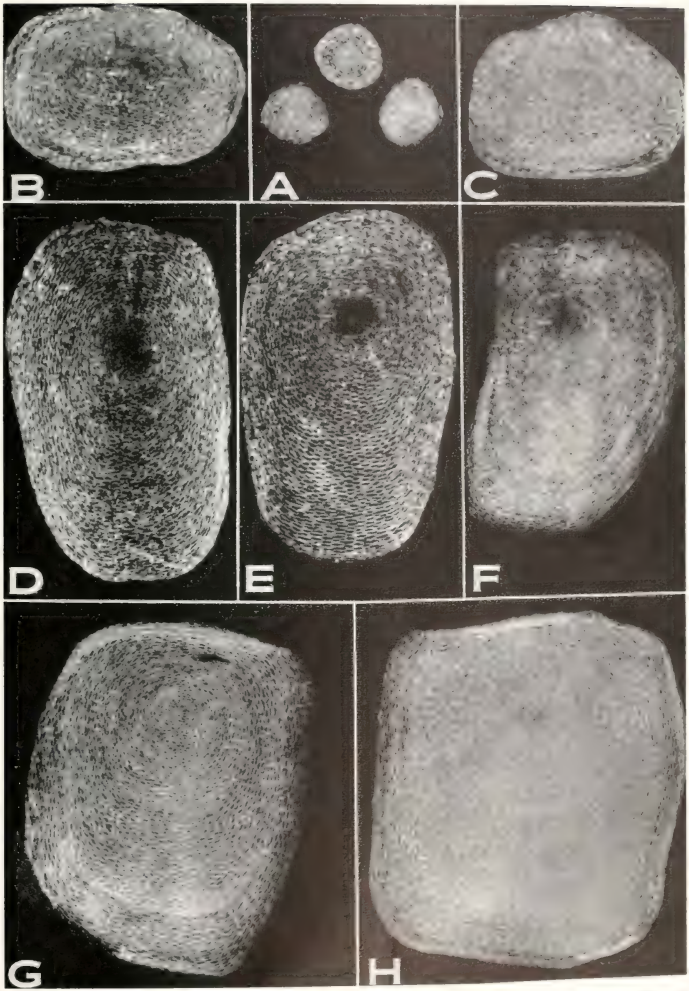

Fig. 4. *Caecilia volcani* sp. nov. A. Subdermal scales from connective tissue. B-C. Dorsal scales from near middle of body. D-F. Scales from 50 centimeters anterior to terminus of body. G-H. Dorsal scales from last centimeter of body. All scales enlarged to same extent. Actual size of two largest, 1.9 × 2.1 mm (G) and 2.0 × 2.35 mm (H). The subdermal scales measure 0.17 to 0.25 mm.

KEY TO CAECILIANS KNOWN IN PANAMÁ AND THE CANAL ZONE

1. Four dental series present 2
   Three dental series present (no splenials) 8
2. Eye covered solidly by bone, visible or invisible externally 3
   Eye in an open socket, visible (or invisible) externally 5
3. Head yellowish; body generally slender, the width in length, 40-60 times; grooves of primary folds edged with black; primaries, 169-189; secondaries, 16-31 ..... *Oscaecilia ochrocephala*
   Head not yellowish; body plumper, the width in length, less than 40 times; grooves not distinctly black-bordered 4
4. Primary folds about 119-133; secondaries, 97-117; width in length, 23-32 times. Pacific drainage ..... *Gymnopis multiplicata*
   Primary folds, about 112-124; secondaries, 94-107; width in length, 19-30 times. Atlantic drainage from Nicaragua, Costa Rica and Panamá ..... *Gymnopis proxima*
5. Very large species (to approximately 1000 mm) 6
   Medium large to small species, 300-600 mm 7
6. Primary folds, 108-145; secondaries, 12-37; body width in length, 22-52 times ..... *Caecilia tentaculata*
   Primary folds, 150-186; secondaries, 28-62; length in width, 42-66 times ..... *Caecilia nigricans*
7. Medium large size (600 mm); primaries 226-231; no secondaries; width in length, 83-89 times ..... *Caecilia elongata*
   Length under 300 mm; primaries, 112-124; secondaries, 14-32; splenials, 2-2; width in length, about 30-36 times ..... *Caecilia volcani,* sp. nov.
8. Secondaries reduced (13); primaries to 92; size small (210 mm); width in length, about 22 times ..... *Dermophis parviceps*
   Secondaries more numerous, 40 or more 9
9. Venter white or slightly clouded; primaries, 89-91; secondaries, 40-45; width in length, 21-24 times ..... *Dermophis balboai*
   Venter variable 10
10. On venter and often on sides each fold barred with black; length to 600 mm; width in length, 15-23 times, primary folds, 99-112 ..... *Dermophis mexicanus mexicanus*
    Venter light, plumbeous to grayish olive; primaries, 91-98; secondaries, 68-78; reaches a length of 345 mm ..... *Dermophis gracilior*

TABLE 1. Data and measurements in mm on *Caecilia volcani* sp. nov.
(All specimens in EHT-HMS Collection; from El Valle de Antón, Coclé, Panamá.)

Number	Type 4689 ♂	4690	4691	4692	4693	4694	4695	4696*	4697*	4697A*
Total length	320.	288.	254.	305.	321.	295.	310.	284±	239+	57+
Head width	7.6	8.4	7.	7.4	8.2	7.	8.	7.2	7.8	5.
Body width	10.5	9.1	8.6	9.8	9.	8.	9.1	8.2	9.	5.
Length : width	30.5	32.	30.	30.	36.	37.	33.	—	—	—
Eye to tentacle	3.6	3.7	2.8	3.4	3.8	3.6	3.6		3.6	2.1
Tentacle to nostril	1.4	1.2	1.1	1.3	1.6	1.2	1.6		1.3	0.7
Primary folds	124.	119.	117.	117.	119.	120.	112.	—	91+	—
Secondary folds	32.	25	21.	17.	19.	20.	14.	—	—	—
Premax. max. t.	12-1-12	10-1-10	9-1-9	10-1-10	9-1-9	9-1-9	12-1-12	10-1-10	9-1-9	10-1-10
Prevom. palatine	9-1-9	9-1-9	8-1-8	10-1-10	11-1-11	9-1-9	10-1-10	9-1-9	10-1-10	8-1-8
Dentary	10-10	9-8	10-10	10-10	11-11	10-10	11-11	9-10	10-10	9-9
Splenial	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	2-2	1-1

* Body injured

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A Comparative Morphological Study and Generic Revision of the Augochlorine Bees (Hymenoptera: Halictidae)[1]

GEORGE C. EICKWORT[2]

ABSTRACT

Bees of the subfamily Halictinae have recently come to the attention of biologists because of the intricacies of their nest structures and the gradation from solitary to social behavior found within the group, but study in the Neotropical region has been hampered by the lack of an adequate supraspecific systematic framework. The purpose of this study is to revise the Augochlorini to the generic and subgeneric levels. The Augochlorini is an American tribe of commonly bright green bees, forming the bulk of the Neotropical halictine fauna. To provide a basis for comparison for the augochlorine genera, a study of the external morphology of *Pseudaugochloropsis graminea* (Fabricius) was undertaken, using dried material and specimens preserved in fluid. Exemplar species representing the major augochlorine genera were then compared with *Pseudaugochloropsis* as to externally visible characteristics, and 49 characters were chosen as useful to distinguish genera. Species representing a wide range of variation within each known augochlorine genus were then compared with the exemplars as to these characters to provide the bases of the generic and subgeneric descriptions, each genus or subgenus thereby becoming an operational taxonomic unit. A numerical analysis was undertaken to aid in estimating overall phenetic affinities of the genera and subgenera. Character states were coded from the generic and subgeneric descriptions, and the data were clustered by the unweighted pair-group method of arithmetic averages; both correlation and distance matrices and phenograms are presented. Twenty-four genera and seven subgenera are recognized in the Augochlorini. *Corynurella* and *Indimaugochlora* are described as new genera, and *Neocorynura (Neocorynuroides)*, *Augochlora (Oxystoglossella)*, *Augochlora (Mycterochlora)*, *Caenaugochlora (Ctenaugochlora)* and *Megommation (Megaloptina)* are described as new subgenera. *Collochloza* Moure is reduced from

[1] Contribution No. 1426 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

[2] Present address: Department of Entomology and Limnology, Cornell University, Ithaca, New York 14850.

generic rank to a subgenus of *Corynura,* and *Paraugochloropsis* Schrottky is removed from synonymy to become a subgenus of *Augochloropsis. Corynuroides* Sandhouse, *Micraugochlora* Schrottky, *Rivalisia* Strand and *Temnosomula* Ogloblin are placed in synonymy. A key to the genera and subgenera is presented. *Corynurella mourei* and *Andinaugochlora micheneri* are described as new species, and *Augochloropsis (Paraugochloropsis) metallica* (Strand) is proposed as a new combination for *Rivalisia metallica* Strand, and a lectotype of the latter species was chosen. Seven more-or-less well-defined generic groups centered around *Corynura, Rhinocorynura, Neocorynura, Augochloropsis, Augochlora, Pseudaugochloropsis,* and *Megaloptidia* were recognized according to phenetic and probable cladistic relationships, and include all genera except *Thectochlora, Megalopta, Chlerogella,* and *Temnosoma.* A phylogenetic scheme is proposed wherein the *Corynura* group is the most primitive, and *Augochloropsis, Augochlora, Megalopta* and the *Megaloptidia* group, and *Temnosoma* represent end-points of evolutionary lines.

INTRODUCTION

This study provides a classification at the generic and subgeneric levels of the Augochlorini, an American tribe of commonly bright green halictine bees. The Augochlorini are distinguished from other American Halictinae principally by the absence of a pygidial plate and ventrally visible surface of metasomal tergum VII and the presence of a spiculum on sternum VIII of the males, and the presence of a median slit on the pseudopygidial area of tergum V of the females. The tribe will be more completely characterized in a companion paper (Eickwort, in preparation).

Bees of the subfamily Halictinae have recently come to the attention of biologists because of the discovery of the intricacies of their nest structures and the behavioral patterns involved in their construction, and because of the gradation from solitary to social behavior found in the group. The Neotropical halictines have been studied biologically principally by Dr. C. D. Michener and his associates, and these bees have contributed important data leading to theories of the origin of social behavior and evolutionary trends in nest structure. The comparative structure of nests of Halictinae has been exhaustively reviewed by Sakagami and Michener (1962), who separated the predominantly Neotropical genera and gave references to publications concerning their nesting biology. It is apparent from this review that the genera have been in need of revision, in order to permit correct placement of species studied biologically and to ascertain whether relationships suggested by nest structure are also evident in the morphological structure of the adult bees.

The bright green halictine bees represent two separate lineages; the majority of the genera, related to *Augochlora,* which I am calling the Augochlorini (characterized briefly above and in greater detail in a companion paper); and a smaller number of genera related to *Agapostemon* and *Caenohalictus,* more similar to the cosmopolitan *Halictus-Lasioglossum* com-

plex. The *Agapostemon* group is still under study and is excluded from the present paper. The separate status of the Augochlorini was recognized by Vachal (1911), who called the group the *Halicti hexagoni*, but his grouping has not been recognized by subsequent authors.

Augochlorine bees are known only from the New World and are the most abundant Neotropical halictines, some representatives ranging outside the tropics to Canada and Chile. Many species are brilliant green in color, which accounts for the common name of "green bees," although other species are dull metallic greenish or black.

To provide a basis for comparison for the augochlorine genera, a study of the external morphology of one species, *Pseudaugochloropsis graminea* (Fabricius), is presented. Thereafter other forms are dealt with, often by comparison with *Pseudaugochloropsis*.

A report on the relationships of morphology to nest structure and social behavior is postponed, so that the non-augochlorine halictine genera can first be adequately studied.

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HISTORICAL REVIEW

The following review deals only with major works concerning the generic classification of Latin American Augochlorini. The systematic history of individual genera is discussed with the description of each genus. This review will not deal with most works on Augochlorini of North America north of Mexico, as these can be easily found through the catalog of North American Hymenoptera (Michener, 1951) and its supplements (Krombein, 1958, 1967).

Fabricius described the first augochlorine bee as *Andrena metallica* in 1793 and later (1804) placed it and two new species in *Megilla.* The first important study of South American Halictinae was by Spinola (1851) on the fauna of Chile, which included his new genus *Corynura,* the first augochlorine genus described.

The groundwork for study of augochlorine bees was laid by Smith (1853) in his catalog of Hymenoptera in the British Museum. Erecting four new genera, he placed 34 species, mostly new, in *Augochlora* (30), *Oxystoglossa* (1), *Megalopta* (2), and *Temnosoma* (1). Other American halictines were placed in *Halictus, Sphecodes,* and *Agapostemon.* He based his new genera principally on wing venation and mouthparts which he illustrated for these genera. In 1879 he published further descriptions of bees in the British Museum, naming species in *Temnosoma, Augochlora, Megalopta,* and *Cacosoma.*

Ashmead, in his classification of the bees (1899), placed *Corynura, Augochlora,* and *Megalopta* (as *Megaloptera*) in the Halictinae, while *Temnosoma* was placed in the Sphecodinae. He placed great weight on wing venation, separating the Panurgidae from the Andrenidae on the basis of the number of submarginal cells. Since the number of cells is variable within

one species or even between wings of one individual in many halictine bees, this artificial subdivision greatly confused later generic descriptions within the Halictinae, although fortunately little affecting the Augochlorini.

The period from about 1890 to 1930 saw great activity in the naming of species of Neotropical Halictinae. Eight authors were especially noteworthy for their contributions: Alfken, Cockerell, Ducke, Friese, Herbst, Schrottky, Strand, and Vachal.

Vachal (1903-1904a,b, 1911) made the first significant attempt at classification of the American halictine fauna. In key form with short diagnoses, he described an immense number of species, all placed in the genus *Halictus*. In 1911 (pp. 9-14), he set forth the divisions and subdivisions of *Halictus* as he used it. He divided *Halictus*, which correspond to the subfamily Halictinae (plus *Sphecodes*) of today, into three divisions, the *Halicti genuini*, *Halicti intermedii*, and *Halicti hexagoni*.

Of these, only the *Halicti genuini* are also found in the Old World: the division coincided with the *Halictus-Lasioglossum* complex and related genera. He described the American species of this division in a different journal (1904b).

The *Halicti intermedii* included *Agapostemon* and its relatives. Vachal divided them into three groups, *Agapostemon*, *Pseudagapostemon*, and his new *Paragapostemon*. Vachal also included the *Halicti rhopali* as a small subdivision of the *H. intermedii*, coinciding with *Rhopalictus*. This subdivision included species currently placed in *Corynura* as well as relatives of *Agapostemon*.

He named his third group *Halicti hexagoni* because of the hexagonal appearance of the faces of the bees, caused by the deeply indented inner orbits of the eyes. This division, corresponding to my concept of the Augochlorini, was distinguished by Vachal as follows: "Orbite interne très fortement sinuée, ou même échancrée; par suite, les yeux sont réniformes et la face paraît hexagone. Yeux très rarement velus (les ex. à yeux velus peuvent-ils être rattachés aux *H. intermedii*?) Face tout au plus duveteuse. Les ♀ ont souvent l'éperon postérieur interne mutique, ayant tout au plus vers la base une dilatation anguleuse comme le talon d'une faux (*H. falcati*) . . . . *H. hexagoni*."

The *Halicti hexagoni* consisted of five subdivisions, the *Halicti megalopti*, *H. coarctati*, *H. vibrissati*, *H. sericei*, and *H. falcati*. The *Halicti megalopti* coincided with *Megalopta* and were characterized by enlarged ocelli and eyes. The *H. coarctati* were characterized by a constriction of the base of the metasoma and end of the mesosoma, and here Vachal included *Caenosoma* (=*Neocorynura*) and *Corynura*. The *H. vibrissati* coincided with *Augochlora* (actually, *Augochloropsis*) and were named for the apical fringes of setae, or "vibrissae," on the metasomal terga.

Vachal defined the *Halicti sericei* and *falcati* on the basis of lack of metasomal vibrissae and the long glossa and equated them to *Oxystoglossa*. He separated *H. sericei* from *H. falcati* on the basis of the hind tibial spurs of the female, pectinate in *sericei*, not pectinate and with an enlarged basal angle in *falcati*. He did not consider this separation to be meaningful division of the *H. hexagoni*, since he could not separate the males. He likewise rejected Schrottky's *Odontochlora*, as the males could not be distinguished. Vachal's *Halicti falcati* largely coincided with *Augochlora* of today, his *H. sericei* with a number of other genera.

Strand (1910) published an outline of the Vachal system which he had received by personal communication from Vachal. Alfken (1926), apparently unaware of Vachal's paper (1911), published a summary in German of Vachal's system, communicated to him by Vachal. This summation, in key form and slightly expanded over Vachal's 1911 publication, is the most easily available and usable source of the system.

Schrottky lived in Paraguay, and his contributions centered on the bees of South America from Brazil southward. Of the workers of his period, Schrottky was the most prolific namer of genera, proposing ten generic and subgeneric names in the Augochlorini. Unfortunately, his generic concepts were poor; he named genera on very few, often insignificant, characters and he consequently split valid genera and artificially lumped others together.

In 1902, he published a monograph on the solitary bees of Brazil, giving keys and descriptions of the genera and species, and he placed all augochlorine species in five genera and subgenera: *Temnosoma, Corynura, Augochlora, Augochlora (Augochloropsis)*, and *Megalopta*. Later, Schrottky was to recognize many more genera. Like most early workers, he used *Augochlora* to refer to bees currently placed in *Augochloropsis*. He named *Paraugochloropsis* for the *Halicti vibrissati* of Vachal and *Pseudaugochloropsis* for the *Halicti sericci*. He split his *Augochlora* into genera and subgenera on the basis of the number of teeth of the tibial spurs, naming the taxa *Paraugochloropsis, Tetrachlora* [replaced by *Augochloropsis* (Schrottky, 1910)], and *Paraugochlora* [a replacement name for *Augochloropsis* as used by Schrottky (1909b)]. Species currently placed in *Augochlora* were placed in his *Odontochlora* (with metasomal sternum I armed in the female) and in *Oxystoglossa*, an artificial group containing species currently placed in several genera. Schrottky (1910) named *Neocorynura* to replace *Cacosoma* Smith, preoccupied, and noted that it was distinct from *Corynura*, but he failed to give adequate separating characteristics. Schrottky also erected four other new monotypic genera and subgenera. He published a summary of his generic concepts (Schrottky, 1909b), which he slightly revised a year later (Schrottky, 1910).

Ducke lived in Brazil, and his studies concentrated on the bees of that country. In contrast to Schrottky, Ducke was conservative in his generic concepts. As summarized in his monograph of the South American bee genera, Ducke (1912) recognized only *Sphecodes*, *Halictus*, and *Megalopta* as valid halictine genera. *Temnosoma* was considered a synonym of *Sphecodes* and other Augochlorini were placed as species groups of *Halictus*. He believed that Vachal had done the best job of dividing American *Halictus* into natural species groups.

Herbst, a resident of Chile, collected and studied the bees of that country. He (1917) published a revision of the bees described by Spinola which included a summary of the lives and expeditions of the early collectors in Chile. In 1922 he published a discussion of the halictine species of Chile, following the revision of Friese (1916b) and placing all species in *Halictus*.

Friese worked with bees from throughout the world and compiled several regional studies and generic revisions. He published a revision of the Chilean Halictinae (1916b), based largely on material collected by Herbst, and placed all species in *Halictus*, since he thought it to be premature to attempt to split the genus. In an account of Costa Rican bees (1916a), he described 52 halictine species, mostly new, placing the augochlorine bees in *Augochlora*, *Corynura*, and *Neocorynura*; he added a few more species in two later addenda (1921, 1925). Friese (1924, 1926) published revisions of *Temnosoma* and *Megalopta*.

Alfken described a number of species of Augochlorini from South America, but his most important contribution (1926) was a revision of the Chilean *Corynura* and discussion of the genus, which included the summary of Vachal's system previously mentioned. Strand (1910) published an account of the bees of Paraguay which included a key to the genera of South American Halictinae. He essentially followed Schrottky, although he identified *Augochlora* with bees we recognize in that genus today and placed *Paraugochloropsis* and *Pseudaugochloropsis* as subgenera of *Augochloropsis*, not of *Augochlora*.

Cockerell's papers on Latin American bees spanned the period from 1896 to 1949, including at least 58 papers dealing wholly or in part with Halictinae. Unfortunately, most of his papers are descriptions and comparisons of limited faunas and seldom are important as revisional studies or clarifications of genera. Among Cockerell's more comprehensive works are two papers on Brazilian bees (1900, 1901) and two papers on the bees in the British Museum (1905a,b), with comments on Smith's and Vachal's species.

Sandhouse (1937) revised the genera and species of augochlorine bees then known to occur in the United States, naming the genus *Augochlorella* for four species and placing four other United States species in *Augochlora* and

Augochloropsis. Her work, the first modern revisional work on augochlorine bees, included some Mexican species and illustrations of genitalia.

From 1940 to the present, Padre J. S. Moure, C. M. F., of Brazil and Dr. C. D. Michener of Kansas and their associates have been the principal contributors to the systematic study of Latin American halictines.

Moure has published at least 23 papers concerning halictines, mostly dealing with the Brazilian fauna. He has clarified and redescribed the augochlorine genera named by earlier workers, especially the artificial groups created by Schrottky; he has also described a large number of new genera. Moure has largely recognized natural groupings, in my opinion, although some of his genera are split rather finely and are considered subgenera or species groups in this paper.

In an important paper, Moure (1943) named the tribe Augochlorini, with type genus *Augochlora*. He equated the Augochlorini with Vachal's *Halicti falcati* and characterized it as having coloration generally metallic, at least in part; the eyes glabrous, deeply emarginate superiorly; pleuro-metaphragmal carinae very short and divergent; marginal depressions little depressed and without vibrissae; internal posterior spur simple.

In the same paper, Moure erected the tribe Augochloropsini, type genus *Augochloropsis*, and equated it with Vachal's *Halicti vibrissati*. He characterized the tribe as having the posterior spur pectinate; males with the 4th sternite provided on each side with a long ciliate appendage; pleuro-metaphragmal carinae parallel or almost parallel; marginal borders of tergites 1-2 generally vibrissate.

Moure presented a key to the South American genera which he placed in the Augochlorini, including *Augochlora, Oxystoglossa, Rhopalictus, Paroxystoglossa, Pereirapis, Ceratalictus,* and *Oxystoglossidia*. This key was later revised (Moure, 1950), substituting *Corynura* for *Rhopalictus, Augochlorella* for *Oxystoglossidia,* and elminating *Oxystoglossa*. Moure's Augochlorini, except for *Corynura,* coincides with a generic group clustered around *Augochlora* in my system, discussed later in this paper; the tribe Augochlorini as used herein is much broader in scope. I consider the Augochloropsini to be included within the Augochlorini.

In the same paper, Moure named the subfamily Megaloptinae for the *Halicti megalopti* of Vachal, characterized by the great development of the eyes and ocelli, and the tribe Megaloptini, type genus *Megalopta* for species with normal maxillary palpi. He included in the Megaloptini the genera *Megalopta, Megaloptidia, Megaloptella, Megommation* and *Tmetocoelia*. Moure stated that he would later name a second tribe for a new genus with elongated maxillary palpi. In later papers, Moure (1951, 1958b) called the new genus with elongated palpi *Ariphanarthra,* but did not create a separate tribe for it, and synonymized *Tmetocoelia* and *Megaloptella* with *Megalopta*.

Moure's Megaloptini is also included within the Augochlorini as used herein, representing a generic group clustered around *Megaloptidia* plus *Megalopta* (see discussion section of this paper).

Among Moure's more important recent papers on Halictinae have been a redescription and generic reassignment of Smith's species of *Megalopta* (Moure, 1958b) and a specific revision of *Paroxystoglossa* (Moure, 1960a). *Paroxystoglossa* remains the only Latin American augochlorine genus of more than two species for which there is an adequate revision. Moure (1964) has recently provided a key to the genera and subgenera of Chilean Halictinae, two of which, *Callochlora* and *Corynura,* are augochlorines.

Michener (1944) placed the augochlorine genera in the Halictinae in his classification of the bees, not giving them separate status.

Michener (1951) in the Hymenoptera catalog listed the North American species of Halictinae and their synonyms, largely following the generic arrangement of Sandhouse (1937). In supplements to the Hymenoptera catalog, Krombein (1958, 1967) followed the generic changes and synonyms given by Michener (1954) and, for eastern North American species, by Mitchell (1960).

In an important revision of the bees of Panamá, Michener (1954) provided a key to the genera and species of Halictinae known from that country, and described many new species and illustrated male genitalia.

Ordway (1966) has recently revised the North American species of *Augochlorella,* including Mexican species not in *Pereirapis.* She presented a key to the genera of green halictines of the United States, including *Augochlora, Augochlorella, Augochloropsis, Agapostemon, Pseudaugochloropsis,* and *Temnosoma.*

Mitchell (1960), in his revision of the species of bees of the Eastern United States, used the generic system of Michener (1954) for augochlorine bees. His work is especially notable for the consistent use and illustration of male genitalia and sterna.

METHODS

External morphology of Pseudaugochloropsis graminea. Both dry pinned museum specimens and material fixed in the field with Dietrich's (Kahle's) solution and preserved in 80% ethanol were used in this study. Illustrations and descriptions were based primarily on dry material, so as to be applicable to other genera for which only dry specimens were available. However, specimens in liquid were compared with dry material for all parts, especially the mouthparts and terminalia.

Dry specimens were relaxed in a moist chamber and the parts to be studied were removed under a dissecting microscope and either glued to cardboard dry or placed in a vial of potassium hydroxide (KOH). The vial was placed in boiling water, and the bee parts when properly cleared were transferred to 35% acid ethanol and then either preserved in glycerin or run through an alcohol series and mounted on a slide in diaphane. All parts which could be studied flattened were mounted in diaphane as permanent slides, for study under a phase microscope or to be drawn with the aid of a microprojector. Material in liquid was dissected in alcohol and the parts examined in alcohol or glycerin.

Illustrations of the following parts were drawn from microprojections of slide-mounted material: antenna, labrum, epipharynx, hypopharyngeal suspensorium, parts of the proboscis, tegula, wings and their basal sclerites, legs (excluding coxae) and associated structures, metasomal sterna, male metasomal tergum VIII plus proctiger, sting and associated spiracle plates, and volsella of the male genitalia. The microprojections were supplemented by phase-contrast observations of the slide preparations and by comparisons with cleared parts in glycerin, parts in alcohol, and dry material.

Special preparatory techniques were necessary for adequate observation of some parts. The mouthparts were removed from a relaxed bee by extending the proboscis from the fossa with the aid of a bent minuten nadel, grasping the base of the labio-maxillary tube with forceps and gently pulling the proboscis loose from the head. The distal parts of the maxillae and prementum were separated from the labio-maxillary tube by grasping the distal parts just distad of the anterior conjunctival thickenings with one pair of forceps while grasping the labio-maxillary tube with another forceps, and gently separating the thickenings from their distal connections. The labio-maxillary tube was slit with a minuten nadel along its membranous lateral areas and the anterior and posterior conjunctival thickenings were mounted separately. The distal parts of the maxillae and prementum were separated basally, and the former were mounted with palpi extended. The prementum was held basally, anterior surface upwards, with one minuten nadel while the blunt edge of a second bent nadel was used to gently pull the glossa to its full extended length. One palpus was removed to expose the paraglossa before the labium was mounted.

The terminal segments of the metasoma were examined by removing the entire metasoma behind segment III, clearing in KOH, and separating the sterna and terga prior to mounting. The sterna were mostly flattened in slide preparations, consequently the dorso-lateral areas do not appear to be bent upwards in the illustrations. However, sternum VI of the female was not flattened on a slide. Sterna VII and VIII of the male were usually dissected as a fused unit. They can be separated only with difficulty by manipulating a minuten nadel between the two sterna, and consequently are illustrated for *Pseudaugochloropsis* and most other genera both as a fused unit and as separate sclerites.

Metasomal tergum VIII plus the proctiger of the male was usually found closely appressed to the inner surface of tergum VII, attached to the gut. With care, the structure could be pulled loose from tergum VII with minuten nadeln. The anal lip of the proctiger is usually folded within the proctiger; it was extended by using the method described in the account of the morphology of *Pseudaugochloropsis*.

The sting was normally dissected as a unit within metasomal sternum VI. The spiracle plates were dissected away from the sting, their connecting membrane severed and they were mounted separately on a slide. The membrane dorso-caudally connecting the two halves of the remainder of the sting was severed so that the sting could be flattened on a slide. For more detailed observations, the shaft was removed from its associated plates.

After examination of the intact male genitalia, they were separated by removing the gonobase, penis valves, and volsellae, and the gonostyli were mounted on a slide for phase-contrast observation. After drawings had been made of the lateral view of the dissected penis valve, the valves and volsellae were also slide-mounted for more detailed observation. Clearing the genitalia in KOH so distorted the penis itself that it was not studied critically.

Illustrations not prepared from microprojections were drawn by observing parts under a dissecting microscope. Drawings were made with the aid of an optical grid; details were added by observation of slide mounts with a phase microscope.

Comparative morphology of the augochlorine genera. Specimens illustrating the range of variation in each named genus as exemplified by obvious external characters were selected from The University of Kansas Snow Entomological Museum and the Michigan State University Entomology Museum collections, with additional material selected from the other collections listed in the acknowledgments. Most of the material was unidentified, although material named to species was consulted where available. When possible, an adequate series of males and females of each species was obtained to provide sufficient material for dissection and detection of intraspecific variation. Thanks largely to the identified material provided to The University of Kansas by Padre J. S. Moure, species of all previously named augochlorine genera were available.

From the species exhibiting the range of variation of each genus, one species was selected as an *exemplar* of the genus on the following bases: availability of a large sample of both sexes; characteristics representative of most species in the genus; species characteristics sufficiently distinctive to insure a conspecific sample; large size for ease of manipulation; specimens belonging to The University of Kansas or Michigan State University, or otherwise accompanied by permission to dissect; and ability to name the species. Since adequate revisions exist for very few of the genera, and since I have not had the opportunity to examine types of most species of augochlorine bees, names could not be applied with certainty to all of the selected species. In large genera with considerable variation, two or three exemplars were chosen. The preliminary selection of species for study led me to select some species as representing new genera and to include these among the exemplars. In small genera with few specimens available, the exemplars could not fulfill all the criteria above, and at times consisted of one specimen.

When material was available, numerous specimens of both sexes of each exemplar species were dissected and the parts mounted in diaphane as permanent slides, as described for *Pseudaugochloropsis graminea*. Nearly every character described for *Pseudaugochloropsis* was compared with that character in each exemplar, and the differences noted. Among the few structures not compared were the epipharynx, the cervix, the hidden portions of the prepectus and second coxa, the ventral region of the mesosoma, and the basal sclerites of the wings, all due to their relative difficulty of preparation. Spot checks of some genera suggested that these structures were not particularly useful taxonomically.

Characters of the exemplar species that differed significantly from those of *Pseudaugochloropsis graminea* were drawn in the same fashion as for *Pseudaugochloropsis*. As nearly as possible, the same parts of different species were all drawn to the same size in the illustrations; thus drawings of each species are likely to be to a different scale. Since there are often large differences in size among species within a genus, size was judged not to be of paramount importance, and illustrating parts so they appear to be of the same size emphasizes differences in proportions which often are important.

Several characters are so important in generic classification that they are illustrated for all or nearly all generic exemplars. These are the hidden male metasomal sterna, the male genitalia, and the face of the female. In contrast, some characters are surprisingly invariable, most noteworthy being the sting apparatus.

As described in the section on characters employed, the exemplar study permitted selection of characters which appeared particularly useful to separate genera. These characters were then examined in each of the species initially selected to represent the range of variation of each genus. Mouthparts were dissected from females and metasomal segments behind segment III were dissected from both sexes, and the parts cleared and studied in glycerin. Temporary glycerin mounts were made of the mouthparts and hidden male metasomal sterna for study under the phase microscope.

This comparative study provided some knowledge of the range of variation in each genus, and led to the recognition of new genera and subgenera which were not originally apparent by their general appearance. While type species were not necessarily used as exemplars, they or species closely resembling them were examined in the comparative study for nearly all genera.

All measurements were made with a Filar optical micrometer mounted upon a dissecting microscope and were based upon dry museum specimens except for the measurements of the mouthparts, which were based upon slide preparations. All measurements are expressed as ratios to eliminate the general size factor.

During the comparative study, a number of unique specimens representing unnamed genera were discovered. However, the description of these genera is not undertaken at the present time. I prefer to wait until further collecting can provide more specimens and both sexes.

Similarly, in some of the large genera a number of individuals exhibited variation that might justify subgeneric status. Usually sexes could not be positively associated, and named species were not involved, to my knowledge. In these cases, naming of subgenera has been

postponed until more specimens confirm their validity, although exceptions to the generic descriptions that these specimens present are noted.

Only those species are described that are necessary to serve as types of new genera and subgenera. Some of these new species may be synonyms of previously named species which I cannot recognize because of inadequate original descriptions. Moure has examined the types of most previously named species and is preparing a catalogue which will give their correct generic positions; species are therefore not listed herein.

The generic descriptions take into account all characters described in the "characters employed" section and follow the same numbering system. When a character is "normal" as described in the section on characters employed, mention of it is usually omitted in the generic descriptions. Thus any numbers missing in a generic description can be assumed to refer to characters which have "normal" states. The particularly important characteristics of each genus and subgenus are italicized. Major trends of variation are noted in the descriptions. Where one or a small group of species differs from the majority in a character or characters, these are listed below the generic descriptions in a separate section as "exceptions." Characters discussed in such sections are marked by asterisks in the generic descriptions.

Generic interrelationships and numerical analysis. The inter-relationships of the genera are not discussed in detail with the generic descriptions, but are considered in a section entitled "Discussion." To aid in the analysis of phenetic similarities, a numerical study was conducted, using the features listed under "Characters Employed." This numerical analysis largely follows the ideas and terminology used by Sokal and Sneath (1963).

The character states were coded from the descriptions of each genus and subgenus, as listed in Table 1 in Appendix 3. Thus each operational taxonomic unit, or "OTU," is a genus or subgenus, and the character states are coded to take into account the range of variation present within the genera and subgenera recognized in this study. This is in contrast to most previous studies, including those of the *Hoplitis* complex of bees (see recent papers by Michener and Sokal, 1966, and Sokal and Michener, 1967), which have used individual specimens or species as OTU's. By using the entire genus or subgenus as the OTU, a certain amount of objectivity has been lost, as there is no opportunity to test if the species placed within a genus are artificially so grouped. One possible alternative, to use every species that differed in any way in any character used, would introduce a prohibitive number of OTU's. Another alternative, to select only one species within each genus or subgenus as an exemplar and use it as the OTU, hides the variation present within many genera. The latter alternative would prove an interesting check on the system I have used, however.

The data matrix was analyzed on the GE 625 computer at The University of Kansas Computation Center, using the "NT-SYS" system developed by Dr. F. James Rohlf, John Kishpaugh, and Ronald Bartcher of The University of Kansas. The program used ("CLST") standardized the data, computed distance and correlation matrices, clustered the OTU's by the unweighted pair-groups method of arithmetic averages, generated distance and correlation phenograms, computed cophenetic value matrices for the two phenograms, and compared the distance and correlation matrices with their cophenetic value matrices. The distance and correlation matrices from this program are included in Appendix 3; the phenograms are redrawn in Figures 417 and 418.

The effects of using different clustering techniques on the same data have been discussed by Sokal and Michener (1967). A similar analysis of many different systems was beyond the scope of this study; the differences between the results based on clustering distances or correlations are noted in the discussion section. Michener and Sokal (1966) have found that stressing one sex or one tagma of a bee can change the results of a numerical analysis; I have attempted to weight both sexes and all tagmata equally (in numbers of characters) so as to minimize this effect.

The results of the numerical analysis are compared with my intuitive concepts of what constitutes "natural" groupings of genera in the discussion section. A high value in the correlation matrix and a low value in the distance matrix both indicate a high degree of similarity between two OTU's.

EXTERNAL MORPHOLOGY OF *PSEUDAUGOCHLOROPSIS GRAMINEA*

The only halictine bee whose external morphology has been studied in detail is *Halictus farinosus* Smith, a North American species not in the Augochlorini. Michener (1944) compared this species, a species of *Sphecodes*, and many non-halictine bees to *Anthophora edwardsii* Cresson.

The present study of *Pseudaugochloropsis graminea* (Fabricius) was undertaken to provide a descriptive basis for comparative morphological studies of augochlorine bees. Its principal concern is the external skeletal anatomy as can be examined conveniently in dried specimens, and it does not purport to advance new evidence as to the evolutionary origin of structures. Terminology and interpretations largely follow that applied by Michener (1944) for *Anthophora edwardsii* and Snodgrass (1956) for *Apis mellifera*, the honey bee. A recent detailed study of the external morphology of a stingless bee, *Melipona marginata*, by Camargo, Kerr, and Lopes (1967), was seen too late for its terminology to be used extensively in this study, although a few new terms introduced by Camargo *et al.* are used for *Pseudaugochloropsis*.

Pseudaugochloropsis graminea was selected as the basis for comparison because: (1) it has the widest range of any augochlorine bee; it or close relatives occur from southern Texas to Argentina, including the West Indies, and are well represented in collections; (2) aspects of its biology are known (Michener and Kerfoot, 1967; Sakagami and Moure, 1967); (3) aspects of its internal morphology have been examined by Brazilian workers (for example, da Cruz Landim, 1967; Urban, 1963); (4) it is comparatively large and easily handled; (5) large numbers of specimens (pinned and preserved in fluid) were available for study; and (6) its taxonomic status was recently clarified by Moure (1960b), who also presented a bibliography for the species. Since that date, Eickwort (1967) has recognized a closely related species in Costa Rica.

In general appearance, *Pseudaugochloropsis graminea* is a brilliant green bee with plumose pubescence that usually does not obscure the body surface. The species is about 9 mm. long. Punctation, color, and general body pubescence are not discussed below.

Several terms used throughout the description merit clarification. General body pubescence is sometimes referred to as "hair" since the hair bases were seldom examined as to articulation; most hairs are probably setae. Short simple setae that occur in well defined groups are often referred to as "sensory setae"; these are frequently found in situations analogous to those described by Lindauer and Nedel (1959) and Markl (1962) for *Apis* and probably function as propioreceptors. Small cuticular rings that resemble pores and do not contain noticeable setae are referred to as "pore-like sensilla."

Female

Head. The head (Figs. 1-4) is slightly wider than long and suborbicular in frontal view and somewhat triangular in profile. The face above the antennal sockets and below the lower margin of the median ocellus may be divided by imaginary vertical lines running dorsally from the outer edges of the antennal sockets into a slightly swollen median *frons* (Fr) (supra-antennal area of Michener, 1944) and lateral *parocular areas* (Pao). The top of the head, or *vertex* (Vx), is continuous with the face and produced into a rounded elevation posterior to the lateral ocelli.

The *clypeus* (Clp) is delimited by an epistomal sulcus which runs between the *anterior mandibular articulations* (amd). The clypeus is slightly convex in profile, the lateral portions curved posteriorly. The *marginal area* (mCl) of the clypeus is depressed, bears a row of long strong setae, and is bounded laterally by produced *clypeal teeth* (toCl).

The epistomal sulcus (interpretation of Bigelow, 1954) is composed of five parts: the horizontal *fronto-clypeal sulcus* (fcs), from which two *dorsal clypeo-genal sulci* (dcgs) extend downward to the elongate *anterior tentorial pits* (atp), and the weak *lateral clypeo-genal sulci* (lcgs) extend from the pits to the anterior mandibular articulations, forming rounded *epistomal lobes* (Esl) of the parocular areas with the dorsal clypeo-genal sulci.

The *subantennal sulci* (sas) (outer subantennal sutures of Michener, 1944) extend from the ventral margins of the antennal sockets to the junctions of the fronto-clypeal and dorsal clypeo-genal sulci, and bound the *supraclypeal area* (Sucl), limited dorsally by a deep dorsally arched impression between the upper edges of the antennal sockets. The supraclypeal area is strongly protuberant, more so than the clypeus, and is rather sharply beveled. The supraclypeal area medially bears the raised *frontal line* (frl) which extends onto the frons. The parocular areas (genae of Snodgrass, 1956) extend ventrally to the clypeus and are bordered medially by the epistomal and subantennal sulci.

The above terminology does not exactly agree with the morphological interpretations of DuPorte and Bigelow (1953) and Bigelow (1954). The frons is considered by them to also include the upper parocular areas and the supraclypeal area, and that usage is followed by Snodgrass (1956) for *Apis*. The subdivisions listed above are taxonomically useful, however. The subantennal sulci are interpreted by them as fronto-genal sutures, and the lower parocular areas as genae. The anterior tentorial pit is interpreted by DuPorte and Bigelow as retaining its position at the junction of the fronto-genal and fronto-clypeal sutures, but in *Pseudaugochloropsis* it is located far ventral to the fronto-clypeal sulcus. Perhaps the dorsal clypeo-genal sulcus represents a fusion of the fronto-genal and fronto-clypeal sutures.

A narrow sclerotized area runs between the anterior and posterior man-

dibular articulations below the eye, the *malar area* (Mal) (gena of Snodgrass, 1956). In lateral view, the *genal areas* (Ge) (postgenae of Snodgrass, 1956) comprise the head behind the eyes and are about as wide as the eyes at their maxima. The genal areas and vertex extend posteriorly to a rounded *preoccipital ridge* (Pror) which surrounds a central strongly depressed area, the *occiput* (Oc). The *occipital foramen* (For) (foramen magnum of Michener, 1944) connects with the cervix, and the *tentorial bridge* (TB) can be seen within. Surrounding the occipital foramen is the *postocciput* (Poc), which is delimited by the *postoccipital sulcus* (pos), containing the *posterior tentorial pits* (ptp). Below and between the tentorial pits, the postocciput forms the *postoccipital bridge* (Pobr) which bears two *setal plates* (sp) which appear homologous to those described by Markl (1962) for *Apis*. Extending ventrally from the base of the postoccipital bridge is a Y-shaped *postgenal suture* (pges) which marks the junction of the *postgenal lobes* (Pgel) to form the *postgenal bridge* (Snodgrass, 1960).

Ventrally the genal areas are extended as *postgenae* (Pge) (Snodgrass, 1960) to the deeply impressed *proboscidial fossa*. The fossa is bordered by *hypostomal carinae* (hsc), which extend medially from the *posterior mandibular articulations* (pmd) to rounded *anterior angles* (ahsc) of the carinae, then posteriorly bordering the fossa to a *posterior flange* (flhs) which surpasses the postgenae and marks the posterior end of the fossa. The posterior half of the fossa, bordered by the hypostomal carinae, has a sclerotized floor and walls and forms the *hypostoma* (Hst). The floor of the hypostoma is marked with the Y-shaped *hypostomal bridge suture* (hsbs); the median portion of the hypostoma between the arms of the "Y" is the *hypostomal bridge* (Hsb). The hypostomal bridge suture joins the postgenal suture. Extending forwards from the anterior angle of the hypostomal carina is the *paramandibular process* (Pamd) which reaches the clypeus and forms the medial border of the *mandibular socket* (MdS). Each paramandibular process is externally strengthened by a flattened carina.

Following the interpretation of Snodgrass (1960), the hypostoma (excluding the hypostomal bridge) could be considered part of the postgenae, continuous with them posteriorly. The hypostomal bridge suture would then be considered a continuation of the postgenal suture, and the hypostomal carinae would be considered secondary strengthening developments, coincident with the proboscidial fossa, as Michener (1944) suggested. The hypostomal bridge, which is lighter in color than the remainder of the hypostoma when viewed in cleared specimens with transmitted light, and the postoccipital bridge, which resembles the hypostomal bridge in transmitted light, could then both be considered remnants of the hypostomal bridge.

The *inner orbit* (ioE) or margin of the *compound eye* (Eye) is deeply emarginate above the level of the antennae. Each eye is clothed with fine

simple hair, about two to five times as long as the diameter of an ommatidium. In the honeybee, Neese (1965) demonstrated that the long eye hairs are sensilla trichodea and help control sidewind deviation during flight. If hairs are removed from only one eye of a worker honeybee, she deviates in the measurement of the sun's angle. Neese also recorded the families of insects in which eye hairs are present, but he did not mention the Halictidae.

The two lateral and one median *ocelli* (O) are arranged in a triangle on the vertex.

The *antennal sockets* are placed midway on the face. Each is surrounded by a narrowly elevated *antennal sclerite* (AnS) and the *antennifer* (af) can be seen within, projecting from the lower median edge, when the antenna is removed. The *antenna* (Fig. 6) is of 12 divisions, the first of which, the *scape* (Scp), comprises over one-third of the total length. The scape is constricted at its base to form a *basal bulb* (bSc) which articulates in the antennal socket. The second division, or *pedicel* (Pdc), is narrowed at its base where it articulates with the scape. The remainder of the divisions form the *flagellum* (Fl).

The scape is partially clothed with long plumose hairs. The basal bulb and the base of the pedicel bear fields of sensory setae comparable to those described by Markl (1962) for *Apis*. The apical portion of the pedicel contains longer simple setae. The terminal nine flagellomeres bear bands of sensory plates (sensilla placodea), with sensory setae intermingled, oriented parallel to the long axis of the flagellum. The flagellar surface is divided into two differently textured longitudinal bands. About 0.4 of the circumference of each flagellomere is occupied by larger, more conspicuous sensory plates, the remainder by smaller, closer, less conspicuous plates. The first flagellomere bears only setae, and the second, setae plus a few scattered plates. The apex of the distal flagellomere is beveled and bears intermingled curved and straight sensory setae. In *Apis,* the sensory plates are arranged in bands occupying about two-thirds the circumference of the distal eight flagellomeres (Richards, 1952). The structure of the apex of the flagellum and its function in cell building in *Apis* was discussed by Martin and Lindauer (1966).

Among the authors who have studied bee mouthparts (see Michener, 1944, for references), Demoll (1908) presented especially detailed illustrations, including European species of Halictinae. Smith (1853) more crudely illustrated mouthparts of four genera of Augochlorini. In the following account of *Pseudaugochloropsis,* "anterior" and "posterior" refer to the surfaces of the downward extended mouthparts.

The *labrum* (Lm) (Figs. 7-8) articulates with the clypeus between the clypeal teeth. Anteriorly the labral *basal area* (baLm) is elevated above the *distal process* (dpLm). The distal process laterally runs to the basal margin of the labrum, largely hidden by the lateral margins of the basal area. The

basal area medially bears a protuberant *basal elevation* (clLm), which bears pore-like sensilla. The distal process is flat and bears a thin median *distal keel* (keLm) which is perpendicular to the process, rounded, and merges with the process at its junction with the basal area. At its lateral margins the distal process bears a row of long flat setae, the *labral fimbria* (fiLm).

The *epipharynx* (Figs. 13-14) projects downwards from the inner wall of the clypeus. It is similar in size and outline to the labrum and lies immediately behind it. The soft white epipharynx is triangular in cross section, the anterior face being slightly concave with a short median longitudinal keel. The posterior swelling medially bears a thin rounded *posterior keel* (pkEp). The posterior swelling bears numerous pore-like sensilla.

The curved *mandibles* (Figs. 9-11) are articulated at the anterior and posterior mandibular articulations below the compound eyes. The *mandibular acetabulum* (acMd) articulates with the condyle at the anterior articulation, and the *mandibular condyle* (coMd) with the posterior articulation. Distal to the swollen basal region, the mandible is somewhat compressed and curved inwards. The mandible bears on its anterior edge a *subapical tooth* (toMd), separated from the remainder of the mandible by *inner anterior* (iaMd) and *outer anterior grooves* (agMd). An *outer diagonal ridge* (drMd) runs from the acetabulum towards the apex of the mandible. An *outer posterior groove* (pgMd) is bounded by an *outer posterior ridge* (prMd). Both the mandibular tip and the subapical tooth may be largely worn away. The mandible bears long hairs on the anterior, posterior, and outer surfaces of the basal region, and in the grooves. The anterior basal region also bears a patch of sensory setae near the acetabulum.

With the exception of the mandibles, the mouthparts are joined into a *proboscis* (Fig. 12) which can be folded into the proboscidial fossa. The basal portion of the proboscis, from its junction with the head to the bases of the prementum and galeae, forms a partly membranous *labio-maxillary tube* (LMT). A detailed analysis of the complicated structure of the proboscis is beyond the scope of this study.

The basal portions of the *hypopharynx* (Fig. 15) are interpreted following Snodgrass (1956). The thin lightly sclerotized *hypopharyngeal lobe* (hlo) is placed medially at the base of the labio-maxillary tube. It appears notched at its base and bifid at its apex, medially it is grooved. Its position and shape are such that the posterior surface of the epipharynx fits snugly into it, the posterior keel of the epipharynx resting in the median groove. Extending into the head from the base of the hypopharyngeal lobe is the *hypopharyngeal suspensorium* (HS), the base of which, the *hypopharyngeal plate* (hpl) (pharyngeal plate of Michener, 1944) bears pore-like sensilla. Extending upwards from the plate are a pair of *oral hypopharyngeal arms* (arm) (pharyngeal rods of Michener, 1944) (Fig. 16); the membrane connecting

these arms bears a poorly defined *median oral plate* (hop). The arms are sharply hooked at their apices.

The anterior portion of the labio-maxillary tube is composed of a complicated series of overlapping sclerites, the *anterior conjunctival thickenings* (ACon), considered a secondary development by Michener (1944). They are illustrated in Fig. 17 but will not be analyzed further. Apically they articulate with the prementum and stipites.

The posterior portion of the labio-maxillary tube (Fig. 18) is bordered by a pair of strong *cardines* (Cd) which basally articulate with the head above the articulations of the anterior conjunctival thickenings and distally articulate with the bases of the stipites. The area between the cardines is sclerotized for about three-quarters of its length from the apex; this sclerotized region was considered a secondary *posterior conjunctival thickening* (PCon) by Michener (1944). Its position and apical articulation with the prementum is analogous to that of a postmentum, and it was considered a submentum by Demoll (1908). Basally the posterior conjunctival thickening joins a membrane which connects with the anterior edge of the hypostomal bridge.

The *stipes* (St) is a long narrow sclerite forming the curved outer edge of the distal portion of the *maxilla* (Mx) (Figs. 19-21). The *galea* (Ga) joins the medial edge of the stipes for about 0.85 of its length and projects beyond it apically. The galea is a thin blade-like structure, convex posteriorly, and provided with an inner ridge. The pointed *postpalpar portion of the galea* comprises about one-quarter of the length of the galea. The outer edge of the galea is rounded and well sclerotized. An *inner strip* (isGa) connects the outer edge with the blade-like medial portion of the galea on its anterior face; it bears crowded thin setae, with a few short stout setae basally. The *maxillary palpus* (MxPlp) arises at the apex of the stipes on the lateral margin of the maxilla from a small membranous area. It is composed of six cylindrical segments, the first and last subequal in length and slightly longer than the other four.

The distal portion of the *labium* (La) (Figs. 22-27) is composed of the *prementum* (Prmt) and the *ligula*. The prementum is an elongate structure whose lateral margins are folded anteriorly and then medially to nearly meet in the midline of the anterior surface. The posterior surface is slightly convex with the median area abruptly more convex; the anterior surface is flattened. Posteriorly the prementum is trilobed apically, the median point joining the *subligular plate* (Sli). Rods inserted posteriorly meet the *ligular arms* (lia) which curve anteriorly to form the lateral margins of a triangular anterior plate, the *salivary plate* (Slp) ("hypopharynx" of Demoll, 1908). The apex of the salivary plate is V-shaped and laterally bears pore-like sensilla. A pair of conspicuous dark *anterior longitudinal braces* (alb) run parallel to and below the salivary plate and meet the ligular arms near their apices; they are

swollen basally and terminate at the level of the base of the salivary plate. The *salivarium* (Slv) opens in the membrane on the anterior side at the base of the salivary plate.

The ligula is composed of two paraglossae and an elongate median glossa. The *paraglossae* (Pgl) are thin, two-segmented structures arising anteriorly at the sides of the salivarium. The basal segment is darkly pigmented medially, and bears a row of strong setae at its base. The distal segment is membranous and narrow and clothed with long cuticular hair-like projections.

The *glossa* (Gls), when fully extended, is a narrow elongate structure comprising about 40% of the total length of the ligula plus prementum. Posteriorly a *median groove* (grGl) runs the length of the glossa, containing a transparent, hard, flexible glossal rod (*Zungenbeine* of Demoll, 1908). The glossal cuticular hairs are long and plumose, arranged in bands similar to those of *Apis* (Snodgrass, 1956), and are longer and fewer per row on the posterior surface, where they border the median groove. The tip of the glossa is pointed and unmodified. The glossa can be considerably contracted in length, and both the glossa and paraglossae can be partially retracted into the apex of the prementum in a manner similar to that of *Apis* (Snodgrass, 1956).

The *labial palpi* (LbPlp) arise laterally on the posterior surface just beyond the apex of the prementum. The first segment of the palpus is longer than the next two together and strongly flattened. The distal three segments are cylindrical.

The entire proboscis can be folded into the proboscidial fossa, with the labrum folding over the apical portions, in turn covered by the mandibles which cross over it. The tips of the galeae are folded back directly beneath the labrum. The posterior median area of the prementum and posterior edges of the stipites form the remainder of the exposed proboscis, with the palpi and tip of the glossa also exposed from beneath the labrum (Fig. 5).

Connecting the head with the thorax is a membranous *cervix* which contains a small, weakly sclerotized median ventral *cervical sclerite*.

Mesosoma. The second tagma of bees consists of the thorax plus the first abdominal segment and is called the *mesosoma* (Figs. 28-33), following Michener (1944). A recent paper by Daly (1964) has added greatly to our knowledge of the morphogenesis of the thorax of *Apis*. The interpretation of the hymenopteran thorax has been subject to controversy, especially concerning the ventral region (see Richards, 1956, and Daly, 1964, for reviews).

The *pronotum* is attached to the mesothorax; it is short dorsally but expanded laterally below the tegulae. The *dorsal surface* (dlN) of the pronotum is distinctly concave, seen in lateral view, shiny, and margined with a raised cream-colored *pronotal lip* (lNlp). At its anterior lateral corners, the pronotum is produced as obtuse *lateral angles* (laN) and continued laterally in nearly straight lines as carinate *dorsal ridges* (drN), which end on the

produced *pronotal lobes* (Lobe) (posterior lobes of the pronotum), covering the first thoracic spiracles. The dorsal surface of the pronotum is separated from the *lateral surfaces* (lsN) by sharply rounded *lateral ridges* (lrN), extending ventrally from the lateral angles. The lateral surface is sharply set off from the anterior surface of the pronotal lobe by weakly impressed lines. Below the pronotal lobes, the pronotum is narrowed and extends ventrally as *postcoxal processes* (1Pc) which nearly meet behind the first coxae.

The remainder of the prothorax, the *prepectus* (Prp) (Fig. 29), is not immovably fused to the mesothorax and is partially concealed by the pronotum. Laterally the *propleuron* is divided diagonally by a transverse *propleural sulcus* (tsPl) into a concealed *lateral portion* (llPl) and exposed *ventral portion* (vlPl). The transverse sulcus terminates posteriorly as a ridge bordering a submarginal groove. The *occipital process* (ocp) projects cephalad from the propleuron and articulates with the postocciput. The occipital process bears sensory setae (Lindauer's organ of Camargo et al., 1967) similar to those of *Apis,* as described by Lindauer and Nedel (1959). The posterior dorsal angle of the lateral portion is prolonged into a *marginal apodeme* (maPr).

The *prosternum* (1S) is partially hidden by the propleura; it projects posteriorly as a triangular plate between the coxae, bearing the *prosternal apophyseal pit* (ap1S). The exposed plate is rimmed by carinae and depressed medially to form a *median groove* (mg), and is expanded laterally beneath the coxae.

The mesothorax is separated from the pronotum by the *first intersegmental groove.* The largest sclerite of the mesonotum is the *mesoscutum* (Sct), which is produced into *anterior-lateral angles* (aaSc) meeting the pronotum above the posterior lobes. *Supra-alar carinae* (sac) extend from these angles to the posterior margin of the mesoscutum. Lateral extensions of the mesoscutum, the *pre-axillae* (Prax), terminate in *anterior mesonotal wing processes.* The mesoscutum is impressed by a *median line* (ml) (anteroadmedian lines of Daly, 1964) and a pair of *parapsidal lines* (pf). Anteriorly the mesoscutum is abruptly rounded and the *mesoscutal lip* (2Nlp) overhangs the pronotum.

The *tegulae* (Tg) (Fig. 34) articulate with the preaxillae and cover the anterior wing bases. They are semi-oval, narrower at the anterior ends, and convex above.

The posterior portion of the mesonotum, the *scutellum* (Scl), is separated by the *scuto-scutellar sulcus* (vs) medially and the *transscutal articulations* (trsa) laterally from the mesoscutum. The *axillae* (Ax) are delimited by *axillary sulci* (axs) and terminate in high *axillary crests* (axcr). The *scutellar crests* (sclcr) form flanges behind the axillae and terminate at the *posterior mesonotal wing processes.*

Each *mesopleuron* is bounded posteriorly by the *2nd pleurointersegmental sulcus* (2pis) (second intersegmental groove of Snodgrass, 1956) which runs dorsally from above the second coxae. Dorsally this groove, interpreted as the *horizontal abscissa of the mesopleural sulcus* (hpls) by Michener (1944), runs horizontally beneath the wing to end in a deep *subalar pit*. Extending from this pit to the anterior margin of the mesopleuron is the *transpleural sulcus* (tpls) (Daly, 1964). The *subalar area* (Saa) above the subalar pit is rimmed by marginal and submarginal ridges and contains the *mesopleural wing process*.

A sulcus running ventrally from the subalar pit is called by Michener (1944) the *pre-episternal sulcus* (pres), interpreted by Richards (1956) as a secondary anterior oblique sulcus, the epicnemial sulcus. It anteriorly sets off the *pre-episternum* (Prep) (or epicnemium, or prepectus, Richards, 1956). The pre-episternum is deeply concave bordering the pronotal lobe at the opening of the mesothoracic spiracle; this concavity is hidden by dense hairs. Extending posteriorly from the pre-episternal sulcus is the *scrobal sulcus* (scrs) which ends at the *episternal scrobe* (scr) and is not continued to the second pleuro-intersegmental sulcus. The *hypoepimeral area* (Hyep) lies above the scrobal sulcus; the area below is the lateral face of the *mesepisternum* (2Eps).

Ventrally extensions of the mesepisterna meet at a *median groove* (mg) (discrimen of Michener, 1944) which bears the *mesosternal apophyseal pit* (ap2s). Each second pleurointersegmental sulcus is continued ventrally as the *precoxal sulcus* (prcs) in front of the second coxa, setting off posteriorly the *katepisternum* (Ktep) (interpreted as the trochantin by Richards, 1956) which bears the condyle of the ventral *coxal articulation*. The katepisternum is continuous with a *lateral intercoxal area* (Liex) extending behind the second coxa. A triangular median area at the anterior margin of the mesosternum, interpreted as the *spinasternum* (Ss) (Richards, 1956), bears the *anterior discriminal pit*. The mesepisternum ventro-laterally bears the elliptical *subpleural signum* (sig).

The *metanotum* (3N) dorsally is bounded posteriorly by the *third intersegmental groove* (3is). Laterally the *trans-metanotal sulcus* (t3Ns) separates the striate *dorso-lateral metanotal area* (d3N) which terminates in a crest behind the scutellar crest.

Each metapleuron is traversed by the *horizontal abscissa of the metapleural sulcus* (hpls) which terminates anteriorly in the *subalar pit*, confluent with the horizontal abscissa of the mesopleural sulcus. The *subalar area* (Saa) above the subalar pit is margined by a ridge containing the *metapleural wing process*. Anterior to the wing process and bordering the mesopleural sulcus is a small *peritreme* (Ptr) in front of the metathoracic spiracle. The *metepisternum* (3Eps) below the subalar pit is bordered posteriorly by the

third intersegmental groove containing the *superior* (spt) and *inferior* (ipt) *metapleural pits;* the line below the inferior pit is the *metapleural sulcus* (3pls) while that above is the *third pleurointersegmental sulcus* (3pis), following Daly (1964). The metapleural sulcus nearly joins the second pleurointersegmental sulcus basally, then curves posteriorly to a point above the third coxa. The *meta-pseudosternal area* (3Pst) below the metapleural sulcus is continuous with the meso-katepisternum and the lateral intercoxal area.

A carinate *metasternum* (3S) (Richards, 1956) projects between coxae II. It laterally meets the meso-katepisterna and medially bears the *metasternal apophyseal pit* (ap3S). A *median groove* (discrimen, Michener, 1944) runs anteriorly from the pit to the margin of the plate.

The *propodeum* is the first abdominal segment fused with the thorax; dorsally the subhorizontal *basal area* (BaPr) consists largely of the *propodeal triangle* (Tri) enclosed by lines extending posteriorly from the ends of the trans-metanotal sulci. The propodeal triangle is rugose and without punctures or hairs. Laterally the *anterior propodeal ridge* extends from the anterior end of the propodeal triangle to the metapleural sulcus. The *lateral surface* (LsPr) of the propodeum extends ventrally to the metapleural sulcus and the *lateral submarginal sulcus* (lsms) which bears a deep shiny pit posteriorly. The *lateral marginal area* (LmPr) it sets off joins the meta-pseudosternal area. The *propodeal spiracle* (Sp) is placed vertically on the lateral surface.

The *posterior surface* (PsPr) of the propodeum is abruptly declivous. The apex of the propodeal triangle extends onto it and ends at the deep *propodeal pit* (ppit). The *posterior marginal area* (PmPr) joins the lateral marginal area at a sharp angle and extends medially to the propodeal pit. Two *propodeal teeth* (th) enclose a circular opening above the fossa. *Apical scales* (asc) are formed below the lateral marginal areas. Strong *lateral carinae* (lcPr) arise at the junctions of the lateral and posterior marginal areas and extend dorsally, diverging slightly and demarking the posterior surface for slightly over half its length. Deep, shiny, oval *posterior submarginal pits* (smpit) border the posterior marginal areas. The posterior marginal areas bear simple hairs which partially obscure the pits. Ventrally the propodeum is largely membranous; small weakly sclerotized areas of the *propodeal sternite* (SPr) occur laterally near the apical scales.

The wing venation of many halictines has been illustrated and utilized in connection with taxonomic works. The homologies of wing veins are in doubt and several interpretations have been proposed, as discussed by Michener (1944). The wings of *Pseudaugochloropsis* (Figs. 35-36) are labeled according to Michener's (1965) interpretation of Ross's system.

Following Michener (1965), I prefer to use morphologically noncommital terms in discussing the following veins and cells of the forewing: *marginal cell* (2nd R_1); *submarginal cells 1* (1st R_1), *2* (1st R_s), and *3* (2nd R_s);

transverse cubital veins 1 (anterior branch Rs), *2* (1st r-m, should be 2nd r-m according to Daly, 1964), and *3* (2nd r-m, should be 3rd r-m, according to Daly, 1964); and *recurrent veins 1* (1st m-cu) and *2* (2nd m-cu). Of special note are the length of the marginal cell and its narrowly truncate and appendiculate apex (Fig. 37), the relative lengths of the submarginal cells, and the arcuate third transverse cubital vein. The first recurrent vein may be received in either the second or third submarginal cell, or may be interstitial with the second transverse cubital vein.

The wing membrane is covered with short erect simple hairs, shorter and denser apically. The wings are traversed by a number of longitudinal creases, the most important of which are shown by dotted lines in Figs. 35 and 36. These creases cause apparent breaks, or pale spots, called *alar fenestrae*, in the veins they cross. Other lesser creases do not "break" the veins. In the forewing, the *submarginal crease* (smcr) crosses the lower ends of the first and second transverse cubital veins and upper end of the second recurrent vein at alar fenestrae. The *vannal fold* (vf) crosses two veins to end at a *vannal incision* in the wing margin. The *jugal lobe* is represented by a very small extension of wing membrane at the base of the forewing. In the hindwing, a corresponding *submarginal crease* (smcr) crosses vein r-m. The *vannal lobe* and *jugal lobe* are distinctly incised and set off by the *vannal* (vf) and *jugal folds* (jf).

The *frenal fold* (frf) of the vannal area of the forewing is sclerotized and turned under, and serves to engage hooks (hamuli, Figs. 38-39) on the costal margin of the hindwing. A series of about 4 very small slightly curved *subbasal hamuli* (bHam) occur about midway between the base of the hindwing and the junction of vein Rs, and a series of 7 or 8 larger, distinctly hooked *distal hamuli* (dHam) occur at and beyond the junction of Rs. As noted by Stavely (1862) and Walter (1907) in other Halictinae, the distal hamuli are not in a continuous evenly spaced series, but rather are clumped.

The basal sclerites of the fore and hind wings are very similar to those illustrated by Michener (1944) for *Anthophora* and Snodgrass (1956) for *Apis*, and are illustrated and labeled in Figs. 40 and 41. The basalares, subalares, and mesopostnotal sclerite (axillary lever of Snodgrass, 1956) are not illustrated. In the forewing, the *median plate* (m) is heavily sclerotized and is the only green sclerite in the wings. Areas of sensilla occur on the bases of the wing veins under the humeral and median plates in the forewing and on the radial and costal sclerites (bases of the veins) in the hindwing.

The legs of females of *Pseudaugochloropsis* (Figs. 42-44) are modified in a number of ways, mostly associated with pollen collecting and nesting behavior. The hairs, especially those of the scopa, are variously branched. Brauc (1913) has described the scopal hairs of European halictines and other bees in

some depth and presented a classification of hair types. The present study mentions hair configuration only in passing.

Coxae I articulate close together behind the prosternum. They are concave and shiny on their outer surfaces, the concavities lined by carinae. Coxa II (Fig. 45) is elongate; its upper portion is concealed by the pleuron and the upper articulation is immediately beneath the inferior metapleural pit, according to Michener (1944). The projecting apex of coxa II is set at a sharp angle from the base of the coxa anteriorly but merges with it posteriorly; it is concave and shiny on its outer surface and carinate posteriorly. The hidden base of the coxa is cut by a diagonal groove, notched near the base. Coxa III is not carinate.

Trochanter I is flattened on the posterior surface, and the upper and lower edges are narrowly rounded. Trochanter II is swollen on its upper edge, and somewhat compressed with both edges broadly rounded. Trochanter III is compressed similar to trochanter II, with long plumose scopal hair similar to that of femur III.

Femur I is swollen on its lower surface, the upper part of the posterior surface is flattened and the anterior surface flattened and concave apically. The upper edge is narrowly rounded and the lower edge broadly rounded, somewhat flattened and sharp-angled basally. Femur II is less swollen on its posterior lower surface; its lower edge is narrowly rounded apically, and basally flattened and sharp-angled. It bears a row of stiff setae, the *mesofemoral brush* (brFm), on the base of its anterior surface. Femur III is rounded on all surfaces, swollen basally on the upper surface, and somewhat flattened posteriorly. Long, plumose, tangled, scopal hair arises on the upper and anterior surfaces. The hair structure (Fig. 47) is of type Vc of Braue (1913), recorded by him for *Halictus* femora.

The tibiae of all legs bear movable spurs (sp) at the lower edges of their apices. The basic structure of a spur, as shown in Figs. 51 and 52, consists of a hollow sclerotized tube with two rows of serrations arising on its inner lateral corners (facing the leg). The posterior (inner) row of serrations may be variously modified.

Tibia I is narrowed basally, broadly rounded on its upper and anterior surfaces. The low posterior surface is flattened. Apically tibia I bears a modified spur (Fig. 49), the *fibula*. The inner row of serrations of the fibula is modified basally to form a broad thin transparent *velum,* directed posteriorly. The rest of the spur is termed the *malus*.

Tibia II is shaped similarly to tibia I. It bears a row of stiff, curved, blunt setae on the lower edge of the anterior surface, the *mesotibial comb*. (cbTb). A single apical *tibial spur* articulates anteriorly.

Tibia III is slightly swollen posteriorly, gradually rounded anteriorly, with a sharply angled upper edge. The lower edge is flattened, shiny, and hairless

basally, rounded with long plumose hairs apically. The anterior and posterior surfaces are spiculate with stiff setae. The lower anterior edge bears long plumose hairs (Fig. 48), forming part of the scopa. Braue (1913) records these hairs as type Vb from tibiae of European halictines and Stockhammer (1966) illustrates them for *Augochlora* and also the stout hairs on the upper edge of the tibia, whose function he discusses.

The hind tibia bears two apical spurs, the posterior or *inner tibial spur* is modified by a row of four or five elongate, narrowly rounded teeth formed from the inner row of serrations. The serrations of the *outer tibial spur* are unmodified, although the spur is curved at its apex. In species of some augochlorine genera, the apex of tibia III is slightly prolonged into *tibial spines* on the anterior and dorsal surfaces, but well-developed spines are absent in *Pseudaugochloropsis* and were not systematically studied in other genera.

A hairless *basitibial plate* (Fig. 46) is raised above the surface of tibia III. The anterior edge extends to the tibial articulation, while the posterior edge runs to the base of the tibia. The function of the basitibial plate in a North American halictine is discussed by Batra (1964).

The tarsi are five-segmented, consisting of the *basitarsus* (Btar), nearly equal in length to the remaining tarsomeres combined, the *mediotarsus* of tarsomeres two to four (Mtar), decreasing in length apically, and the longer *distitarsus* (Dtar), which bears the pretarsus at its apex. The basitarsi are strongly compressed and set at an angle in relation to the tibiae, with the lower edge directed anteriorly. The surfaces of the basitarsi are spiculate and clothed with stiff setae, denser posteriorly, and the apices of all basitarsi and mediotarsi bear spine-like setae. Shiny depressions, the *basitarsal pits* (Trpt, Fig. 49), occur at the bases of all basitarsi. The distitarsi are slightly depressed dorso-ventrally and covered with fine setae, denser on the lower surfaces.

Basitarsus I bears a shiny semicircular depression at its base on the anterior surface, the *strigular concavity* (Steav). It is lined with a row of wide blunt setae, the *strigular comb* (Comb), which projects posteriorly. This concavity plus the tibial fibula comprise the *strigilis* (Fig. 49) or antenna cleaner, whose function is described by Snodgrass (1956) for *Apis*. The anterior basitarsus is more broadly rounded on its posterior than on its anterior surface and the lower edge is narrowly rounded. Its upper edge is sharp-angled and somewhat carinate and produced apically into a *distal process* (dp), which overlaps the mediotarsus. This edge is lined with a distinct row of flattened setae, the *anterior basitarsal brush* (brTr, Fig. 50), quite noticeable when the basitarsus is viewed with the edge facing the observer. This brush was also described by Sakagami and Wain (1966) for an Indian halictine, and a possible function is discussed by Batra (1968) for a North American halictine.

The structure of the middle tarsus agrees with that of the fore, except that

the basitarsus is not carinate nor produced apically on its upper surface and does not bear a basitarsal brush.

The hind tarsi are more strongly compressed, both surfaces being only slightly rounded and both edges sharp. The setae on the posterior surface are particularly strong and dense, forming a *tarsal comb,* while the setae on the upper edge of the basitarsus are pectinate, similar to those of the tibial edge. The basitarsus is produced apically into a *distal process* (dp) which bears a dense brush of hairs on its anterior surface, the *penicillus* (pen) (posterior basitarsal brush of Michener, 1944). Batra (1964) named this structure and described its function for a North American halictine. The hairs comprising the penicillus are of an unusual structure (Fig. 56), spatulate and usually fringed at the ends. Braue (1913) described similar hairs as type X in the penicillus of *Anthophora.*

The *pretarsi* of all legs resemble closely those of *Apis* (Snodgrass, 1956) and *Anthophora* (Michener, 1944) and are labeled accordingly in Figs. 54 and 55. The camera of Michener is called the *arcus* (Arc) by Snodgrass, likewise the auxilium is termed the *auxiliary sclerite* (Aux). The *manubrium* (Mn) of Snodgrass (orbicula of Michener) is elongate and tapers apically, bearing two pairs of long plumose setae in addition to smaller basal setae. The *claws* or ungues are subapically toothed on their inner sides and bear two pairs of long setae on their lower surfaces, the proximal pair of which is pectinate, in addition to smaller setae. The mechanism of the pretarsus is described by Snodgrass (1956).

Metasoma. Following Michener (1965) the abdomen behind the propodeum is termed the *metasoma,* and the metasomal segments are numbered from one on. The metasoma is oval (Fig. 64), broadest at the third metasomal segment, and tapered apically. Six *metasomal terga* are visible externally, the last nearly hidden. The terga bend strongly downwards and inwards laterally and overlap the sterna. The six externally visible *metasomal sterna* are much flatter and exposed only ventrally.

Metasomal tergum I (Figs. 87-88) is strongly narrowed basally to form the *petiole* which articulates with the mesosoma. The anterior margin of the petiole bears a strong transverse ridge, the *petiole acrotergite* (Act). A *median petiole plate* (Ptpl) (vertical plate of Michener, 1944) projects anteriorly to articulate with the propodeal teeth. The base of the median plate is set in a depression at the base of the *median sulcus* (ms). To either side of the median plate on the petiole neck are patches of sensory setae (Nedel's organ of Camargo et al., 1967), whose function was described by Lindauer and Nedel (1959) for *Apis.* The mechanism of the petiole was described by Snodgrass (1956) for *Apis.* Metasomal tergum I consists of three surfaces: the *anterior surface* (an) bears long erect hairs; the *dorsal surface* (do) bears appressed hairs; and the *ventro-lateral surfaces* (vl) overlap metasomal

sternum I laterally and are set off from the anterior and dorsal surfaces by *ventro-lateral lines* (vll). The anterior surface bears a pair of *spiracles* (Sp.) The *posterior marginal area* (pma) is depressed.

Metasomal terga II to IV (Figs. 89, 57 58) are similar in structure. Basally a tergum is margined by an internal ridge, the *antecosta* (An), which terminates in *tergal apodemes* (Ap) before the lateral margins of the tergum. The tergal apodemes are located progressively nearer the lateral margins and become progressively larger in more posterior terga. The *gradulus* (Grd) separates the anterior *pregradular* (Prga) from the posterior *postgradular area* (Poga). The pregradular area projects slightly over the postgradular area, and a membrane lined with fine hair-like microtrichae, the *gradular lip* (grl), hangs over the postgradular area. The graduli of terga III and IV have *gradular angles* (gra) laterally, and then extend posteriorly. Posterior extensions of the graduli progressively increase in length in more posterior terga. The *spiracles* (Sp) are located just lateral to the gradular angles and are hidden by overlapping terga. The *ventro-lateral areas* (vl) of the terga overlap the lateral margins of the corresponding sterna. The postgradular areas are depressed just posterior to the graduli and also on the *posterior marginal areas* (pma).

The postgradular area of metasomal tergum V (Figs. 59-60) apically is covered with long plumose hairs, the *prepygidial fimbria*. The thin *pseudopygidial area* (Ppa) extends from a median invagination of the more heavily sclerotized and pigmented postgradular area and is densely covered with setae, shorter and not plumose on either side of a *median slit*. The apical margins of the tergum, from about below the posterior extensions of the gradulus to the lateral edges of the pseudopygidial area, are bordered with a row of strong *latero-marginal setae*.

Metasomal tergum VI (Figs. 61-63) is considerably smaller than V and narrowed apically. The gradulus is reduced, not angulate, and ends laterally distant from the spiracles, with a very small lip. Medially the gradulus ends to either side of a heavily sclerotized, protuberant *suprapygidial plate* (Supg), which is narrowed at a transverse ridge and continued apically to expand into a thick truncate *pygidial plate* (Pyg). The postgradular area is clothed with long dark plumose hairs, the *pygidial fimbria*. The posterior marginal area is thin and hairless except for fine setae on the margin; it terminates medially on the inner surface of the pygidial plate. The pregradular area is clothed with fine hairs above the suprapygidial plate. Batra (1964) illustrated terga V and VI and discussed their function in a North American halictine.

Metasomal sternum I (Figs. 87, 98) anteriorly forms the ventral surface of the petiole. The V-shaped *antecosta* (An) sets off a narrow *acrosternite* (Acs), which laterally bears patches of sensory setae comparable to those whose function is discussed by Lindauer and Nedel (1959) for *Apis*. The

basal area (ba) of the postgradular area is elevated medially and bears short setae on either side, as well as a poorly defined *median line* (ml). The graduli extend only laterally. The long plumose postgradular hairs of sterna I and II and to some extent those of more posterior sterna form a supplementary scopa.

Metasomal sternum II (Fig. 65) is margined anteriorly by the strongly notched antecosta, which terminates at the *sternal apodemes* (Ap). The gradulus extends medially and posteriorly below the apodemes. Laterally the *dorso-lateral areas* (dlS) are expanded into thin flaps which extend dorsally beneath the overlapping tergum. On either side of the midline, the pregradular area bears patches of sensory setae. The postgradular area basally bears very short setae where sternum III overlaps, more apically it bears long plumose setae, longest just before the depressed posterior marginal area.

Metasomal sterna III to V (Figs. 66-68) are similar, progressively decreasing in size. The antecosta forms a strong internal ridge and extends across the bases of the sternal apodemes, which are considerably larger than those of sternum II and bear upturned *dorsal processes* (dp). A narrow *acrosternite* (Acs) is anterior to the antecosta. There is no gradulus, and the "pregradular area" does not bear distinct patches of sensory setae, although there are very fine setae near the antecosta. The setae of the "postgradular area" are similar to those of sternum II.

Metasomal sternum VI (Figs. 69-70) is narrowed posteriorly to a rounded apex, and the dorso-lateral areas are strongly curved upwards inside tergum VI. The antecosta is developed only laterally and the sternal apodemes are directed mesally. The gradulus is only weakly defined near the apex.

The genital segments are confined within the genito-anal chamber formed by tergum and sternum VI. Metasomal segments VII and VIII are modified to form the ovipositor or *sting,* very similar in structure to those of *Apis* (Snodgrass, 1956) and *Anthophora* (Michener, 1944, 1956). Figures 71 to 76 illustrate the sclerotized portions of the sting, using the morphologically noncommital terminology of Snodgrass; Michener's terms are cited in parentheses following. The *spiracle plates* (Fig. 72) (metasomal hemitergites VII) are joined by membrane and lie lateral to the sting; they are removed in Fig. 71. The sting proper consists of a pair of *oblong plates* (Ob) (2nd valvifers) which are overlapped by the *quadrate plates* (Qd) (metasomal hemitergites VIII). Articulating with both plates is the *triangular plate* (Tri) (1st valvifer). Two pairs of *rami* (r) connect the valvifers with their respective valvulae. The *shaft* (Stng, Fig. 76) of the sting is composed of a central *stylet,* the fused second valvulae, which are enlarged basally to form the *bulb* of the sting. The stylet is closely appressed by a pair of *lancets* (Lan) (first valvulae) which basally are expanded into *valves* (Vlv) which lie within the bulb. Dorsally the Y-shaped *furcula* (Figs. 73-74) (stylet apodemes) surmounts the bulb. The sting *sheaths* (Sh) (gonostyli) lie to either

side of the shaft at rest and articulate with the oblong plates. Medially they are concave and membranous, laterally sclerotized with abundant plumose setae apically and stronger setae near their bases. Metasomal tergum IX (not illustrated) is represented by a lightly sclerotized area above the anus, bearing sensilla. The mechanism of the sting in *Apis* was described by Snodgrass (1956).

Male

The male of *Pseudaugochloropsis graminea* differs from the female in many minor characteristics, such as punctation, pubescence, color, and proportions of structures, but these are not dealt with below. Only structures which differ from those of the female in a significant way are described.

Head. The male head (Figs. 77-78) is narrower below; the clypeal margin is without a marginal row of strong setae and the clypeal teeth are shorter. Posteriorly, the postgenal lobes (Fig. 80) meet at the posterior flange of the hypostomal carinae. Ventrally, the hypostomal lobes also meet at the posterior flange. The para-mandibular processes are thinner extensions of the hypostoma, lacking the flattened carinae of the female. The mandibular sockets are considerably narrower.

The antennae (Fig. 79) are longer in the male and composed of 13 segments. The scape is comparatively shorter, comprising less than one-fifth of the total length. The flagellum is somewhat flattened and nearly devoid of sensilla on its lower surface; the terminal flagellomere is hooked and bare at its apex.

The basal area of the male labrum (Figs. 81 and 82) merges gradually into the distal process. The basal elevation extends nearly the width of the basal area, has no sharply differentiated apical face, and is invaginated medially. The distal process lacks a keel.

The male mandible (Figs. 83-84) is simpler than that of the female. The subapical tooth is lacking, although the anterior grooves and ridge are present. The outer posterior groove and the diagonal ridge are also lacking.

Mesosoma. The hair is generally less dense and shorter on all leg surfaces in the male. On the fore leg, the upper edge of the basitarsus is not prolonged into a distal process, nor is it carinate, and there is no basitarsal comb.

On the middle leg, the lower edge of the femur is not flattened basally and does not bear a mesofemoral brush. The mesotibial comb is present but poorly formed of shorter, straighter, weaker setae.

The hind leg (Fig. 85) does not bear a scopa, consequently the hairs are considerably shorter and less dense. The femur is not as swollen, lacks the dense long scopal hairs, but exhibits a flattened dull area at the base of the anterior surface which bears short, fine, simple hairs. The basitibial plate is only weakly indicated by a shiny hairless area. The inner tibial spur (Fig. 86) is not pectinate, although some of the serrations of the inner row are

enlarged distally. The distal process of the basitarsus is not as produced and lacks the penicillus.

Metasoma. The principal external differences between the sexes of **Pseudaugochloropsis** lie in the metasoma, especially the genitalia. The male metasoma (Fig. 97) is relatively narrower than that of the female and consists of seven externally visible terga and six externally visible sterna. Terga III and IV (Figs. 90-91) differ slightly from those of the female as to the gradulus; the gradular angle is less prolonged, and the posterior extensions of the gradulus are shorter.

Metasomal tergum V (Fig. 92) is not as narrow posteriorly and lacks the prepygidial fimbria and pseudopygidial area. The gradulus follows the trend established in III and IV. Tergum VI (Fig. 93) lacks all modifications connected with the pygidial area, including the pygidial fimbria. The gradulus is not produced at the gradular angles and is very slightly extended posteriorly.

Metasomal tergum VII (Figs. 94-95) is the last externally visible tergum. It is relatively short, with the lateral areas bent sharply back from the dorsal area and not overlapping a sternum. The rounded tergal apodemes are at the extreme corners and only slightly produced beyond the level of the antecosta. A gradulus is lacking; the "pregradular area" is sharply delineated from a nearly vertical "postgradular area," seen in lateral view. The "postgradular area" bears long plumose setae apically.

Metasomal tergum VIII (Fig. 96) is normally concealed beneath tergum VII in the roof of the genito-anal chamber. It is a small mostly membranous structure, only the lateral tergal apodemes being well sclerotized, connected by a ventral membrane. The structure of this tergum and its posterior extension, the *proctiger* (Pr) of metasomal segment IX, was analyzed by Snodgrass (1941) for other Apoidea, and his analysis is followed here. The proctiger extends as a membranous tube enclosing the hindgut from the posterior extensions of tergal apodemes VIII. It bears a weakly sclerotized *subanal plate* (Sban) on its ventral floor. The posterior margin of the ventral membrane, the *anal lip* (Anl), is fringed with finger-like *post-anal filaments* (fil), brownish extensions of the membrane covered with hair-like microtrichae. Normally the filaments are folded into the proctiger, the subanal plate then situated at the apex of the proctiger. The filaments can be everted by probing with a minuten nadel between the dorsal and ventral membranes from the anterior end of the proctiger. In dry specimens, the filaments are occasionally seen everted and protruding beneath the apex of tergum VII.

Sternum II (Fig. 99) is similar to that of the female, but relatively longer, and the gradulus extends nearly to the posterior margin. The apodemes of sternum III (Fig. 100) lack well-defined dorsal processes and also lack the acrosternite. The gradulus extends anteriorly nearly to the antecosta and posteriorly nearly to the posterior margin; a well-defined gradular lip is pres-

ent. The postgradular area is largely clothed with short setae. The setae are longest laterally just anterior to the posterior marginal area.

Metasomal sternum IV (Fig. 101) resembles sternum III but possesses a distinctive hair arrangement. Most conspicuous is a V shaped median patch of dense erect setae, extending from the posterior margin to a basal patch of short setae.

Metasomal sternum V (Fig. 102) is broadly emarginate posteriorly. The gradulus meets the antecosta medially, and the antecosta does not extend across the bases of the sternal apodemes. The postgradular area is nearly without setae basally, and posteriorly bears two conspicuous setal patches. The posterior marginal area is strongly depressed. This sternum was illustrated by Eickwort (1967).

Metasomal sternum VI (Fig. 103) differs considerably from that of the female and more nearly resembles sternum V of the male. The dorso-lateral areas are bent sharply upwards. The gradulus broadly joins the antecosta. The posterior marginal area is strongly depressed and notched medially. The postgradular area bears dense long setae posteriorly, but is nearly without setae basally.

Metasomal sterna VII and VIII (Figs. 104-106) are small weakly sclerotized structures hidden beneath sternum VI in the genito-anal chamber and closely associated with the genitalia. Sternum VIII lies above sternum VII and is fused to it laterally, so that the two appear to be one structure when dissected and are separated only with difficulty. Sternum VII is narrowly tranverse, bearing anterio-lateral sternal apodemes and two thin posterio-lateral projections clothed with short setae at their tips. Sternum VIII is more complex, being a two-layered structure with the layers joined anterio-medially and laterally at their fusion with sternum VII. Anteriorly the sternum is produced into a median keeled *spiculum* (Spc); posteriorly it is bordered by long plumose setae.

The male genitalia of Hymenoptera have been subjected to many interpretations and nomenclatorial schemes. A perusal of this subject is beyond the scope of this study. While usage of a morphologically noncommital terminology would be preferred, a view Michener now shares (Michener, pers. comm.), the terminology originally used by Michener (1944, 1956) is now so widely applied in studies of bee taxonomy that it is followed here. Its usage in this study does not necessarily imply an acceptance of morphological homologies that the terms indicate. Comparative terms used by Snodgrass were cited by Michener (1956). Two studies of hymenopteran genitalia should be cited here: that of Beck (1933) which included an augochlorine bee, and that of Snodgrass (1941), which unfortunately did not include any Halictinae, although many other bees were described. Both studies included

the associated hidden sterna and terga. Michener (1954) illustrated the genitalia of many augochlorine genera.

The *gonobase* (Gb) of the genitalia (Figs. 107-111) ventrally encloses the *genital foramen* by a pair of posteriorly extending *ventral gonobasal arms* (vga). A membranous *ventral gonobasal bridge* (vgb), sclerotized in many other species, connects these arms. A *median sulcus* (ms) denotes the presence of an internal ridge. The *dorsal lobes* of the gonobase slightly overlap the bases of the gonocoxites.

The *gonoforceps* (parameres of Snodgrass, 1957) are complicated structures forming the lateral walls of the genitalia. As they are not divided by an articulation into distal and basal parts, the identity of basal *gonocoxites* (Gcx) and distal *gonostyli* (telomeres of Snodgrass, 1957) cannot be ascertained with certainty. An arbitrary distinction is made in *Pseudaugochloropsis* wherein a transverse ridge dorsally and a diagonal line ventrally separate the distal gonostylus. Similar separations can be made in other augochlorine genitalia.

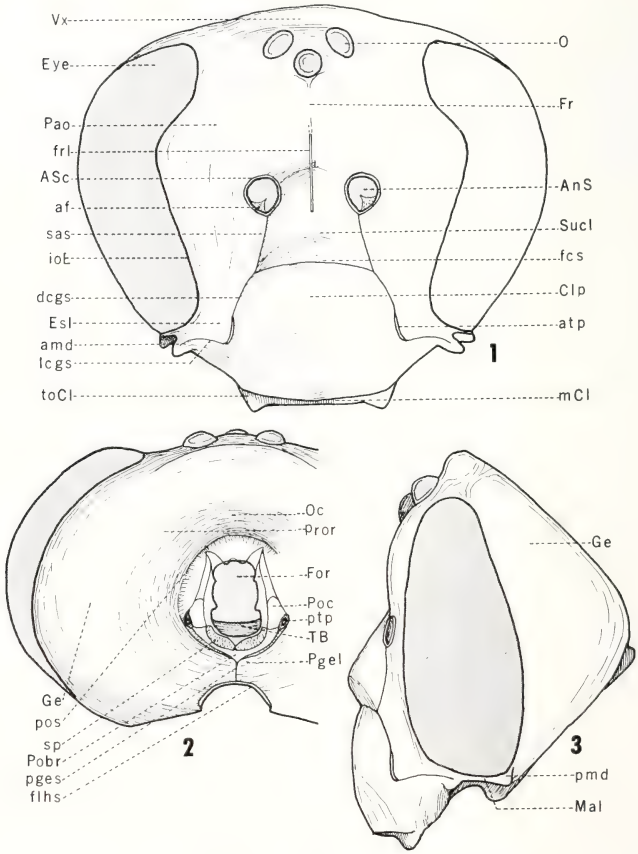
The gonocoxites are joined at their bases by a *dorsal gonocoxal bridge* (dcb). Ventrally, a pair of arms extend medially beneath the ventral gonobasal arms to form the *ventral gonocoxal bridge* (vcb).

Each gonostylus is prolonged as a setose *ventral process* (vst), the medial margin of which is lined with especially thick setae. Extending medially from the ventral inner margin is a thin transparent flap, the *ventral parapenial lobe* (par). The *dorsal process* (dst) of the gonostylus is set off by a membranous area from the apical ridge of the gonocoxite. The dorsal process is produced apically to form a ventrally directed convex surface, bearing short setae. Long setae arise dorsally near the base of the gonostylus. The ventral structure of the gonostylus was illustrated in greater detail by Eickwort (1967).

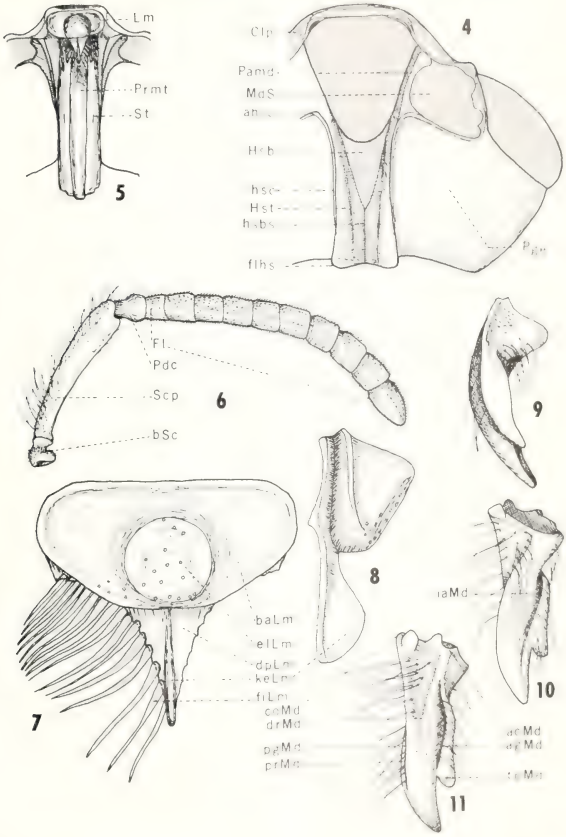
Between the gonoforceps, the *aedeagus* is composed of the *penis* (Pen) which is laterally bordered by a pair of *penis valves* (Pv) (sagittae of Snodgrass, 1957). The penis is entirely membranous and was not studied in detail.

The penis valves (Fig. 111) are heavily sclerotized structures, connected by a small *dorsal bridge* (dbpv), only the posterior border of which is well sclerotized. Each valve bears a *basal median projection* (bmpv) posterior to the *apodeme* (Ap) of the penis valve (aedeagal apodeme of Snodgrass, 1957). Apically, a dorsal transverse depression is continuous with a diagonal groove that runs to the inner edge of the basal median projection. The penis valve is expanded laterally at the level of the transverse depression. A strong *dorsal crest* (dcpv) terminates at the apical end of the transverse groove. The crest is darkly pigmented at its apex and bears short setae, and is longitudinally grooved and carinate. The lateral margin of the penis valve is extended apically lateral to the crest and bears setae. The apex of the penis valve is bent ventrally and pointed. Ventrally the penis valve bears long setae.

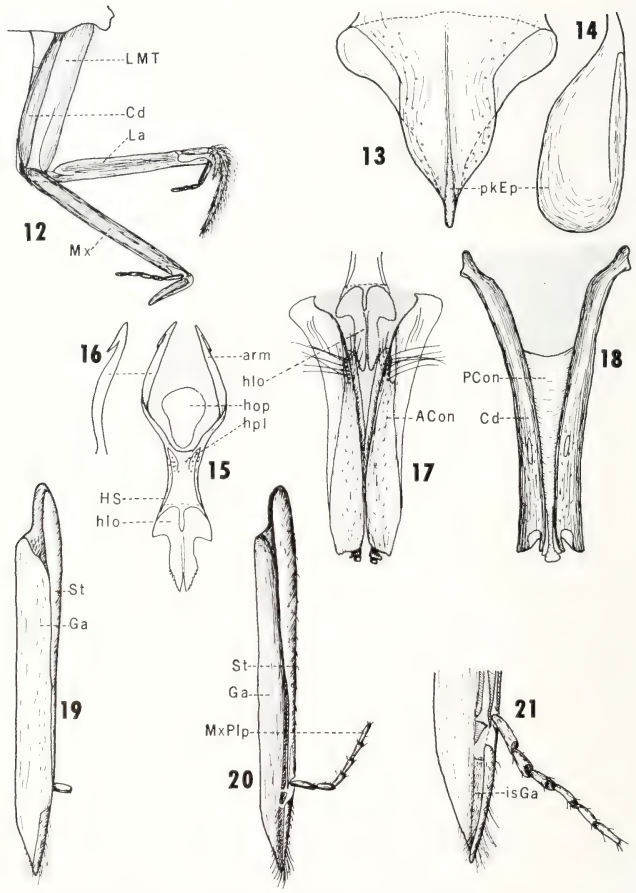
The *volsellae* (Vol, Fig. 110) are two sclerotized plates lying ventral to the penis. Each volsella is notched medially, rounded apically, and laterally indented by a *volsellar notch* (vnt). The volsellar notch separates the slightly movable lateral *cuspis* (Cu) from the median *digitus* (Di). The notch borders are pigmented and bear small teeth; the cuspis border bears very small hairs projecting into the notch. Internally the cuspis is characterized by a strong ridge, and a weaker internal ridge margins the digitus.



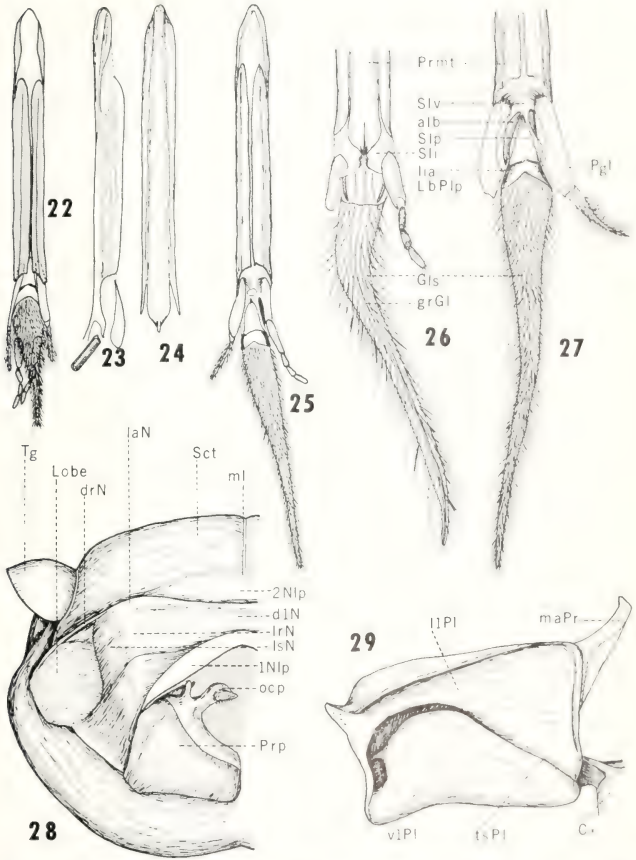
FIGS. **1-3.** Head of *Pseudaugochloropsis graminea* female. **1,** front; **2,** posterior; **3,** lateral. **af**—antenniter; **amd**—anterior mandibular articulation; **Ans**—antennal socket; **ASc**—antennal sclerite; **atp**—anterior tentorial pit; **Clp**—clypeus; **dcgs**—dorsal clypeo-genal sulcus; **Esl**—epistomal lobe; **Eye**—compound eye; **fcs**—fronto-clypeal sulcus; **flhs**—posterior flange of hypostomal carina; **For**—occipital foramen; **Fr**—frons; **frl**—frontal line; **Ge**—genal area; **ioE**—inner orbit of eye; **lcgs**—lateral clypeo-genal sulcus; **Mal**—malar area; **mCl**—marginal area of clypeus; **O**—ocellus; **Oc**—occiput; **Pao**—parocular area; **Pgel**—post-genal lobe; **pges**—post-genal suture; **pmd**—posterior mandibular articulation; **Pobr**—postoccipital bridge; **Poc**—postocciput; **pos**—postoccipital suture; **Pror**—preoccipital ridge; **ptp**—posterior tentorial pit; **sas**—subantennal sulcus; **sp**—setal plate; **Sucl**—supraclypeal area; **TB**—tentorial bridge; **toCl**—clypeal tooth; **Vx**—vertex.



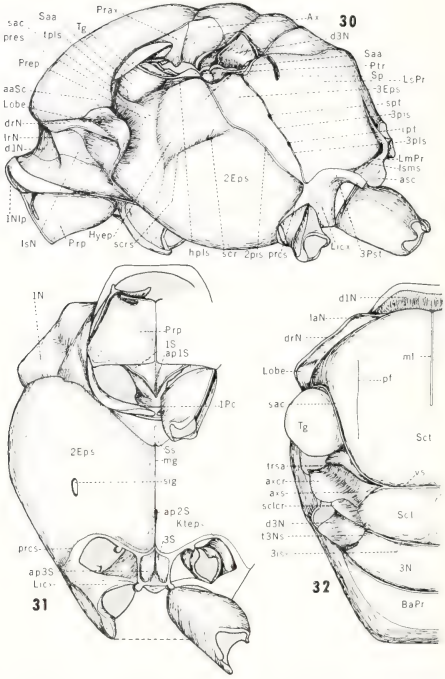
FIGS. 4-11. *Pseudaugochloropsis graminea* female. **4**, ventral view of head: **5**, mouthparts folded into prosocidal fossa; **6**, antenna; **7-8**, labrum (7, anterior; 8, lateral); **9-11**, mandible (9, anterior; 10, inner; 11, outer). **acMd**—mandibular acetabulum; **agMd**—outer anterior groove of mandible; **ahsc**—anterior angle of hypostomal carina; **baLm**—basal area of labrum; **bSc**—basal bulb of scape; **Clp**—clypeus; **coMd**—mandibular condyle; **dpLm**—distal process of labrum; **drMd**—outer diagonal ridge of mandible; **elLm**—basal elevation of labrum; **fiLm**—labral fimbria; **Fl**—flagellum; **flhs**—posterior flange of hypostomal carina; **Hsb**—hypostomal bridge; **hsbs**—hypostomal bridge suture; **hsc**—hypostomal carina; **Hst**—hypostoma; **iaMd**—inner anterior groove of mandible; **keLm**—distal keel of labrum; **Lm**—labrum; **MdS**—mandibular socket; **Pamd**—paramandibular process; **Pdc**—pedicel; **Pge**—paraglossa; **pgMd**—outer posterior groove of mandible; **prMd**—outer posterior ridge of mandible; **Prmt**—prementum; **Scp**—scape; **St**—stipes; **toMd**—subapical tooth of mandible.



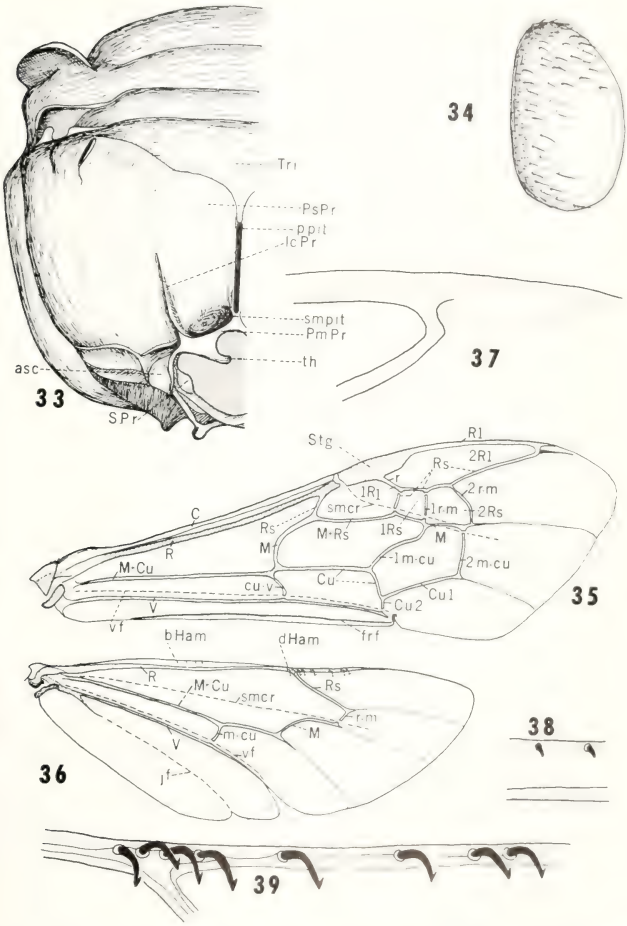
FIGS. 12-21. Mouthparts of *Pseudaugochloropsis graminea* female. **12,** lateral view of extended proboscis; **13-14,** epipharynx (13, posterior; 14, lateral); **15,** basal portion of hypopharynx; **16,** lateral view of hypopharyngeal arm; **17-18,** labio-maxillary tube (17, anterior; 18, posterior); **19-21,** distal portion of maxilla (19, posterior; 20, anterior; 21, anterior view of post-palpal portion of galea). **ACon**—anterior conjunctival thickening; **arm**—hypopharyngeal arm; **Cd**—cardo; **Ga**—galea; **hlo**—hypopharyngeal lobe; **hop**—median oral plate; **hpl**—hypopharyngeal plate; **HS**—hypopharyngeal suspensorium; **isGa**—inner strip of galea; **La**—labium; **LMT**—labio-maxillary tube; **Mx**—maxilla; **MxPlp**—maxillary palpus; **PCon**—posterior conjunctival thickening; **pkEp**—posterior keel of epipharynx; **St**—stipes.



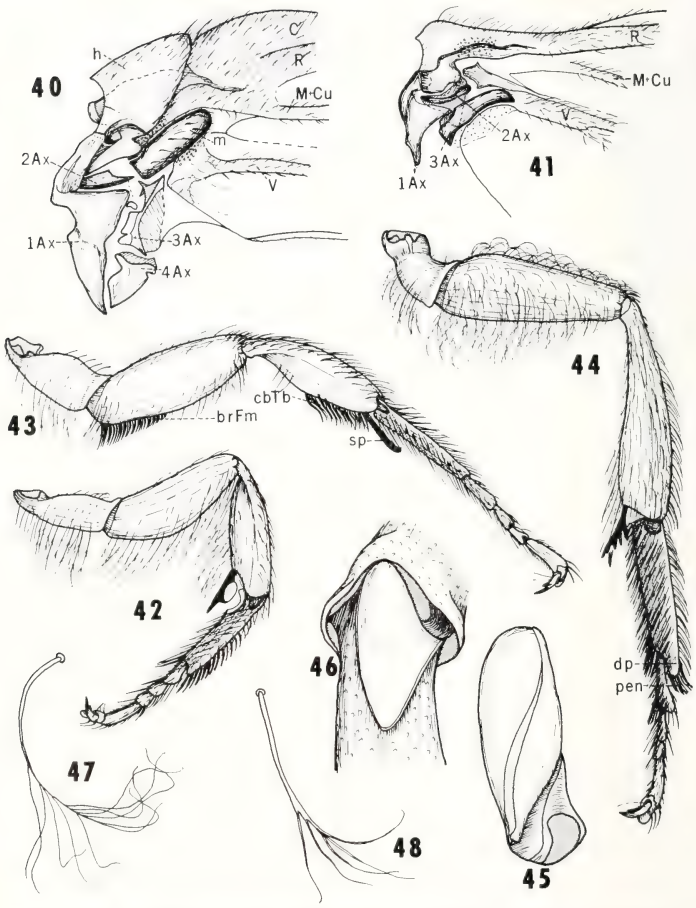
Figs. **22-29.** *Pseudaugochloropsis graminea* female. **22-27,** distal portion of labium; **22,** ligula retracted into prementum; 23-24, prementum (23, lateral; 24, posterior); **25,** ligula extended, anterior view; **26-27,** ligula (26, posterior; 27, anterior); **28,** anterior view of mesosoma; **29,** prepectus. **alb**—anterior longitudinal band; **Cx**—coxa; **d1N**—dorsal surface of pronotum; **drN**—dorsal ridge of pronotum; **Gls**—glossa; **grGl**—median groove; **laN**—lateral angle of pronotum; **LbPlp**—labial palpus; **lia**—ligular arm; **Lobe**—proximal lobe; **l1Pl**—lateral portion of propleuron; **lrN**—lateral ridge of prementum; **lsN**—lateral surface of prementum; **maPr**—marginal apodeme of prepectus; **ml**—median line of mesoscutum; **1Nlp**—pronotal lip; **2Nlp**—mesoscutal lip; **ocp**—occipital plagosa; **Pgl**—pygofer lobe; **Prmt**—prementum; **Prp**—prepectus; **Sct**—mesoscutum; **Sli**—sublateral plate; **Slp**—lateral plate; **Slv**—salivarium; **Tg**—tegula; **tsPl**—transverse propleural sulcus; **v1Pl**—ventral portion of propleuron.



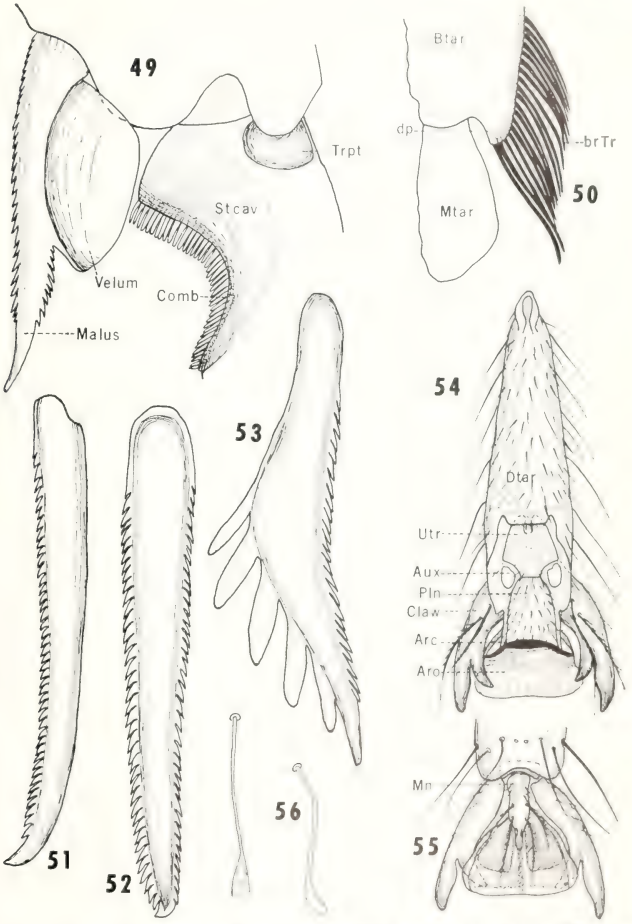
FIGS. **30-32.** Mesosoma of *Pseudaugochloropsis graminea* female. **30,** lateral; **31,** ventral; **32,** dorsal. **aaSc**—anterior-lateral angle of mesoscutum; **ap1S, 2S, 3S**—sternal apophyseal pits; **asc**—apical scale; **Ax**—axilla; **axcr**—axillary crest; **axs**—axillary sulcus; **BaPr**—basal area of propodeum; **d1N**—dorsal surface of pronotum; **d3N**—dorso-lateral metanotal area; **drN**—dorsal ridge of pronotum; **2Eps, 3Eps**—episterna; **hpls**—horizontal abscissas of pleural sulci; **Hyep**—hypoepimeral area; **ipt**—inferior metapleural pit; **3is**—3rd intersegmental groove; **Ktep**—katepisternum; **laN**—lateral angle of pronotum; **Licx**—lateral intercoxal area; **LmPr**—lateral marginal area of propodeum; **Lobe**—pronotal lobe; **lrN**—lateral ridge of pronotum; **lsms**—lateral submarginal sulcus of propodeum; **lsN**—lateral surface of pronotum; **LsPr**—lateral surface of propodeum; **mg**—median groove; **ml**—median line of mesoscutum; **1N**—pronotum; **3N**—metanotum; **1Nlp**—pronotal lip; **1Pc**—postcoxal process; **pf**—parapsidal line; **2pis, 3pis**—pleurointersegmental sulci; **Apls**—metapleural sulcus; **Prax**—pre-axilla; **prcs**—precoxal sulcus; **Prep**—pre-episternum; **pres**—pre-episternal sulcus; **Prp**—prepectus; **3Pst**—metapseudosternal area; **Ptr**—peritreme; **1S**—prosternum; **3S**—metasternum; **Saa**—subalar area; **sac**—supra-alar carina; **Scl**—scutellum; **sclcr**—scutellar crest; **scr**—episternal scrobe; **scrs**—scrobal sulcus; **Sct**—mesoscutum; **sig**—subpleural signum; **Sp**—spiracle; **spt**—superior metapleural pit; **Ss**—spinasternum; **Tg**—tegula; **t3Ns**—trans-metanotal sulcus; **tpls**—transpleural sulcus; **trsa**—transscutal articulation; **vs**—scuto-scutellar sulcus.



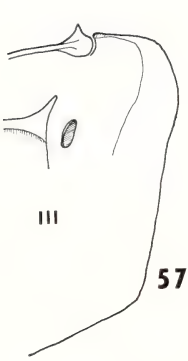
Figs. 33-39. *Pseudaugochloropsis graminea* female. 33, posterior view of mesosoma; 34, tegula; 35, forewing; 36, hindwing; 37, [illegible] 38, subbasal hamuli; 39, distal hamuli. asc—apical scale; bHam—subbasal hamuli; dHam—distal hamuli; frf—frenal fold; jf—jugal fold; lcPr—lateral carina of propodeum; PmPr—posterior marginal area of propodeum; ppit—propodeal pit; PsPr—posterior surface of propodeum; smcr—submarginal crease; smpit—posterior submarginal pit of propodeum; SPr—propodeal spiracle; Stg—stigma; th—propodeal tooth; Tri—propodeal triangle; vf—vannal fold.

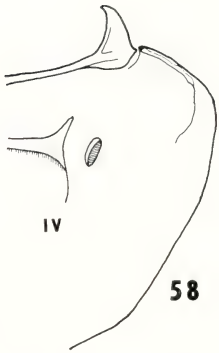


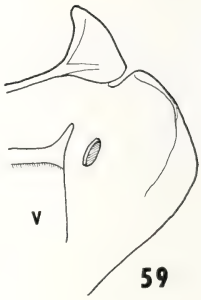
FIGS. 40-48. *Pseudaugochloropsis graminea* female. **40-41,** bases of wings (40, forewing; 41, hindwing); **42-44,** legs, excluding coxae, posterior views (42, fore; 43, middle; 44, hind); **45,** middle coxa; **46,** basitibial plate; **47-48,** scopal hairs (47, of femur; 48, of tibia). **1Ax, 2Ax, 3Ax, 4Ax**—axillaries; **brFm**—mesofemoral brush; **cbTb**—mesotibial comb; **dp**—distal process; **h**—humeral plate; **m**—median plate; **pen**—penicillus; **sp**—tibial spur.

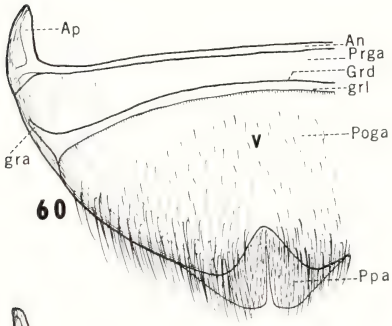


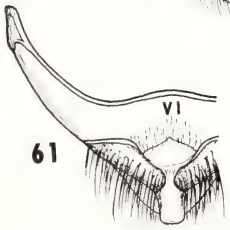
FIGS. 49-56. Legs of *Pseudaugochloropsis graminea* female. **49**, strigilis; **50**, anterior basitarsal brush; **51-52**, outer hind tibial spur (51, lateral view; 52, inner view); **53**, inner hind tibial spur; **54-55**, pretarsus (54, ventral; 55, dorsal); **56**, hairs of pseudolus. **Arc**—arcolus; **Aro**—arolium; **Aux**—auxiliary sclerite; **brTr**—anterior basitarsal brush; **Btar**—basitarsus; **Comb**—strigular comb; **dp**—distal process; **Dtar**—distitarsus; **Mn**—mandible; **Mtar**—mediotarsus; **Pln**—planta; **Stcav**—strigular concavity; **Trpt**—basitarsal pit; **Utr**—unguitractor.

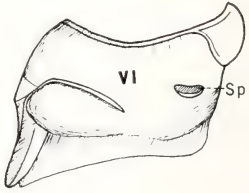




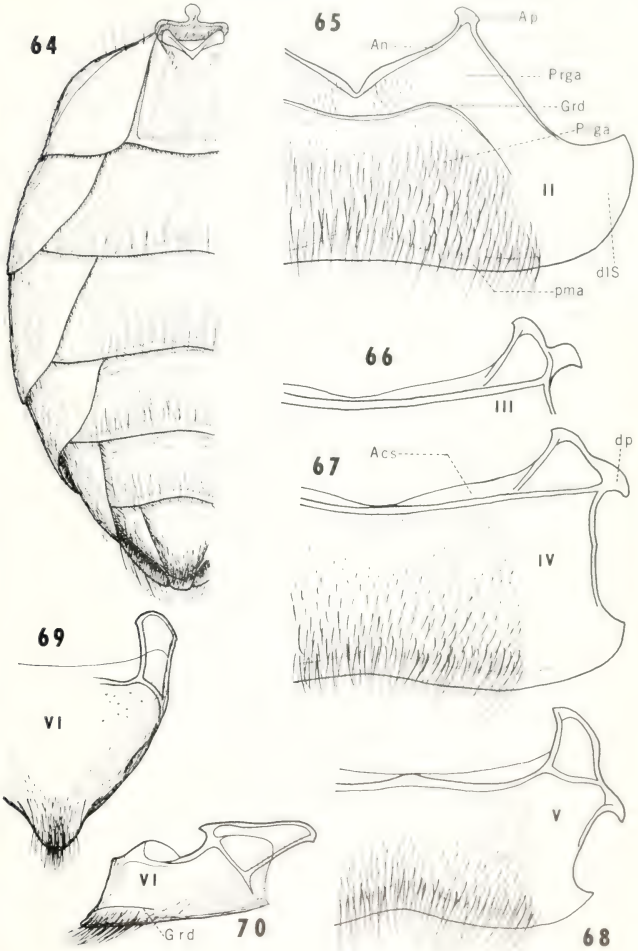




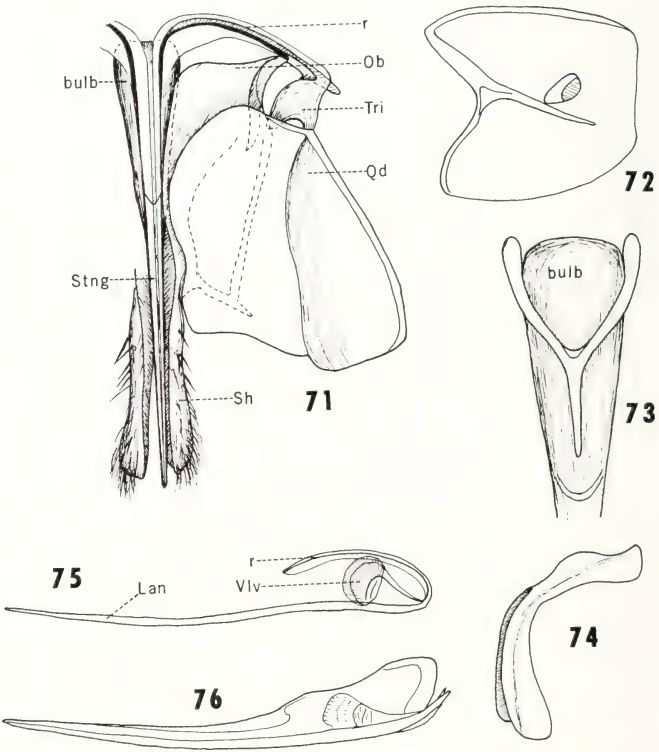




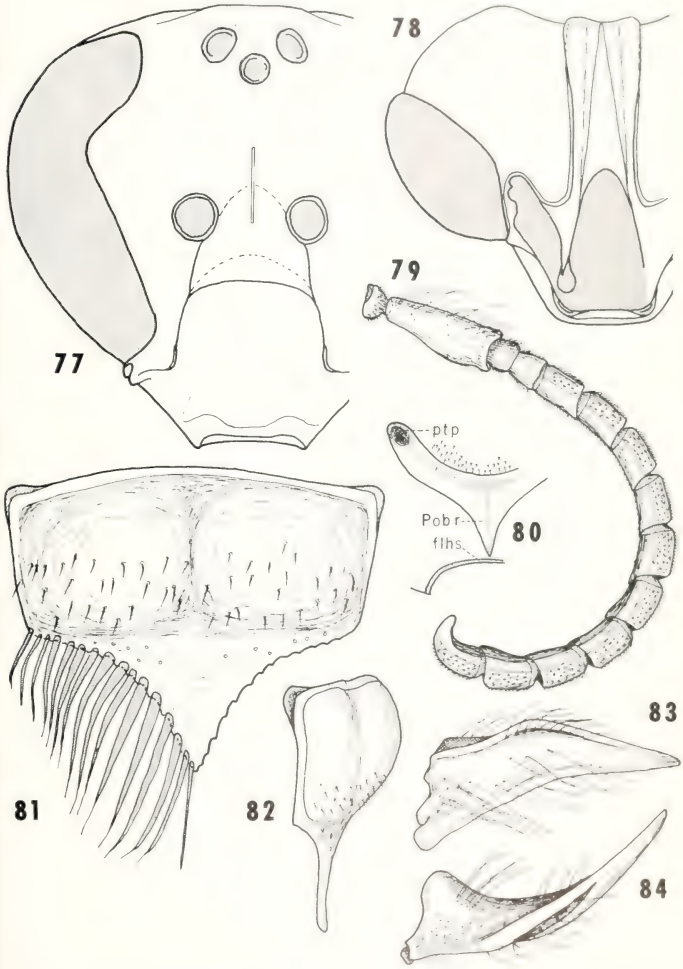
FIGS. **57-63.** Metasomal terga of *Pseudaugochloropsis graminea* female. **57,** tergum III; **58,** tergum IV; **59-60,** tergum V (59, lateral; 60, dorsal); **61-63,** tergum VI (61, dorsal; 62, lateral; 63, pygidial area). Hairs not shown on 57-59, 62-63. **An**—antecosta; **Ap**—tergal apodeme; **gra**—gradular angle; **Grd**—gradulus; **grl**—gradular lip; **Poga**—post-gradular area; **Ppa**—pseudopygidial area; **Prga**—pre-gradular area; **Pyg**—pygidial plate; **Sp**—spiracle; **Supg**—supra-pygidial plate.



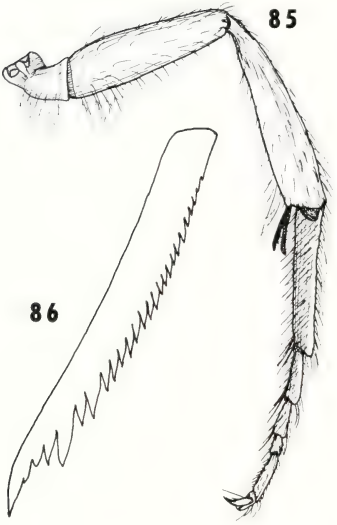
FIGS. 64-70. Metasoma of *Pseudaugochlora graminea* (Fabricius): 64, ventral view; 65, sternum II; 66, base of sternum III; 67, sternum IV; 68, sternum V; 69-70, sternum VI (69, ventral; 70, lateral). **Acs**—acrosternite; **An**—anticosta; **Ap**—apodeme; **dlS**—dorsolateral area; **dp**—dorsal process of apodeme; **Grd**—gradulus; **Poga**—postgradular area; **pma**—posterior marginal area; **Prga**—pre-gradular area.

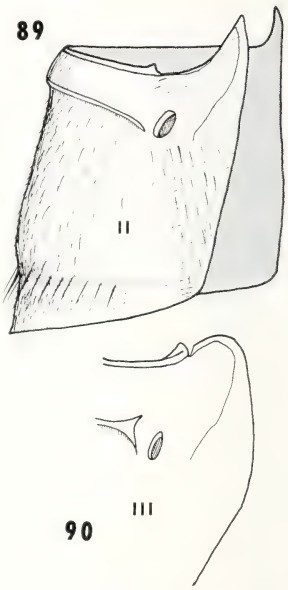


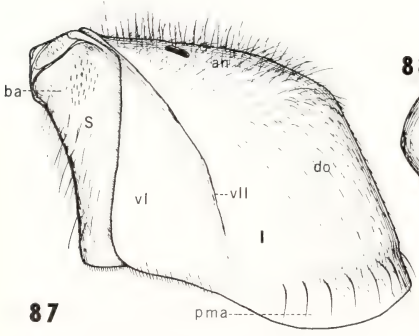
FIGS. **71-76.** Sting apparatus of *Pseudaugochloropsis graminea* female. **71,** sting apparatus, ventral view, flattened; **72,** spiracle plate; **73-74,** furca (73, dorsal; 74, lateral); **75,** first valvula; **76,** sting shaft. **bulb**—bulb of sting shaft; **Lan**—lancet; **Ob**—oblong plate; **Qd**—quadrate plate; **r**—rami; **Sh**—sheath; **Stng**—sting shaft; **Tri**—triangular plate; **Vlv**—valve.

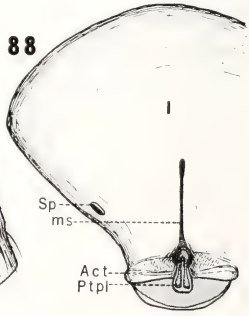


Figs. **77-84.** Head of *Pseudaugochloropsis graminea* male. **77,** front; **78,** ventral; **79,** antenna; **80,** postoccipital bridge; 81-82, Ilium; 81, anterior; 82, lateral; 83-84, mandible (83, outer; 84, anterior). **flhs**—posterior flange of hypostomal carina; **Pobr**—postoccipital bridge; **ptp**—posterior tentorial pit.

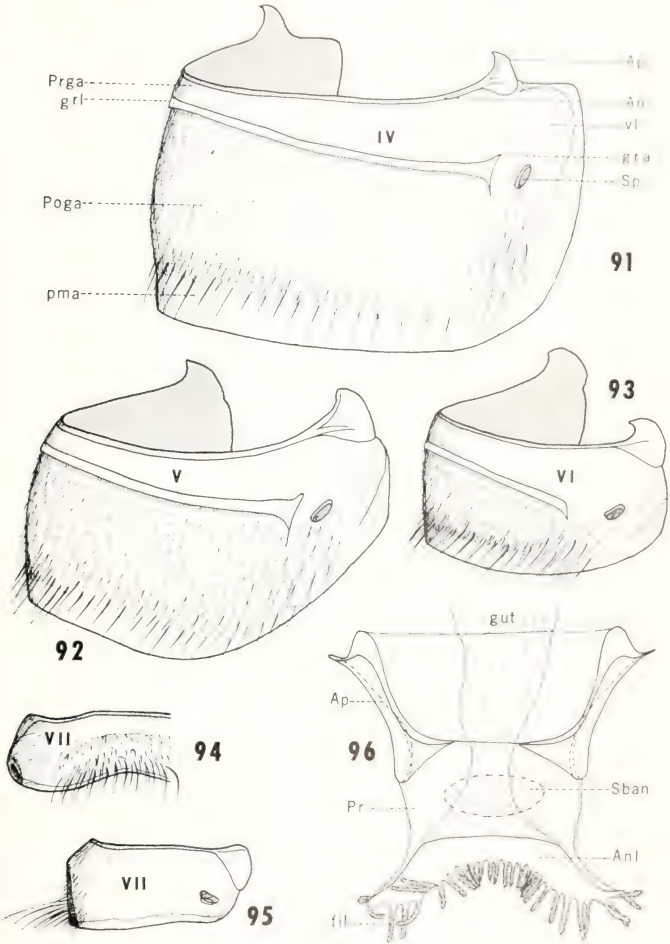




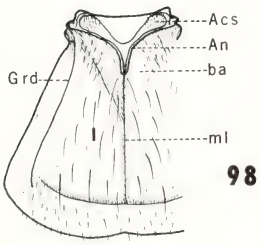


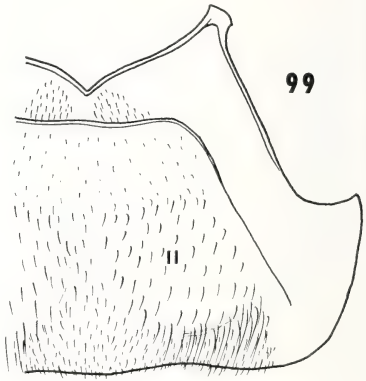


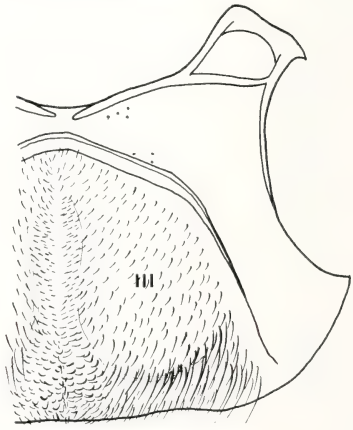
FIGS. 85-90. *Pseudaugochloropsis graminea* male. **85,** hind leg, posterior view; **86,** inner hind tibial spur; **87,** metasomal tergum and sternum I, lateral view; **88,** tergum I, anterior view; **89,** tergum II; **90,** tergum III. Hairs not shown on 88, 90. **Act**—petiole acrotergite; **an**—anterior surface of tergum I; **ba**—basal area of sternum I; **do**—dorsal surface of tergum I; **ms**—median sulcus; **pma**—posterior marginal area; **Ptpl**—median petiole plate; **S**—sternum I; **Sp**—spiracle; **vl**—ventro-lateral area of tergum I; **vll**—ventro-lateral line.



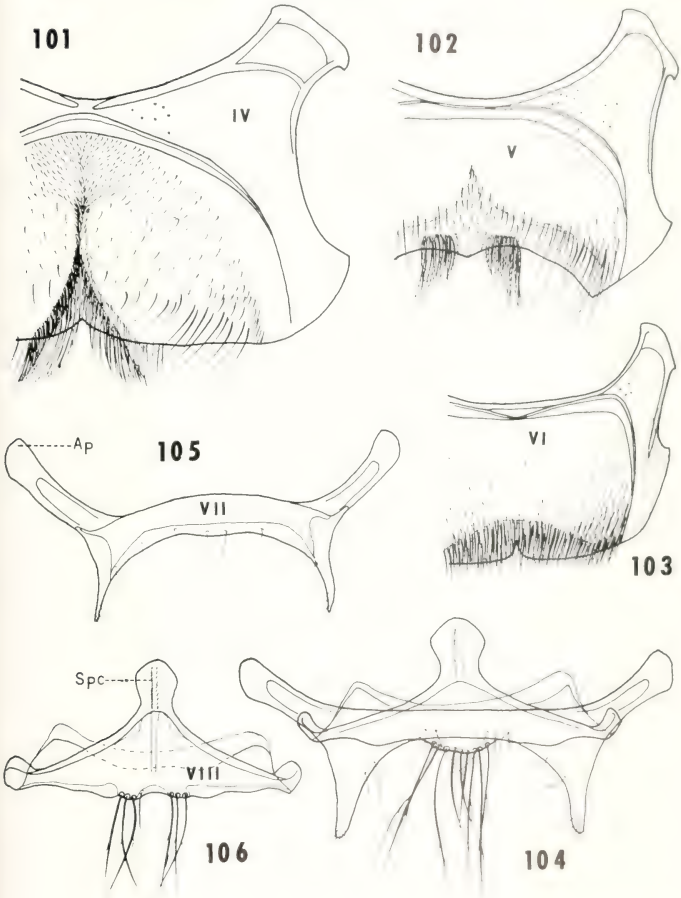
Figs. 91-96. Metasomal terga of *Pseudaugochloropsis graminea* male. 91, tergum IV; 92, tergum V; 93, tergum VI; 94-95, tergum VII [illegible]; 96, tergum VIII and proctiger, dorsal view. An—[illegible]; Anl—anal lip; Ap—apical apodeme; fil—[illegible] filaments; gra—gradular angle; grl—[illegible]; pma—[illegible] marginal area; Poga—[illegible] gradular area; Pr—proctiger; Prga—[illegible]; Sban—[illegible]; Sp—[illegible]; vl—ventro-lateral area.



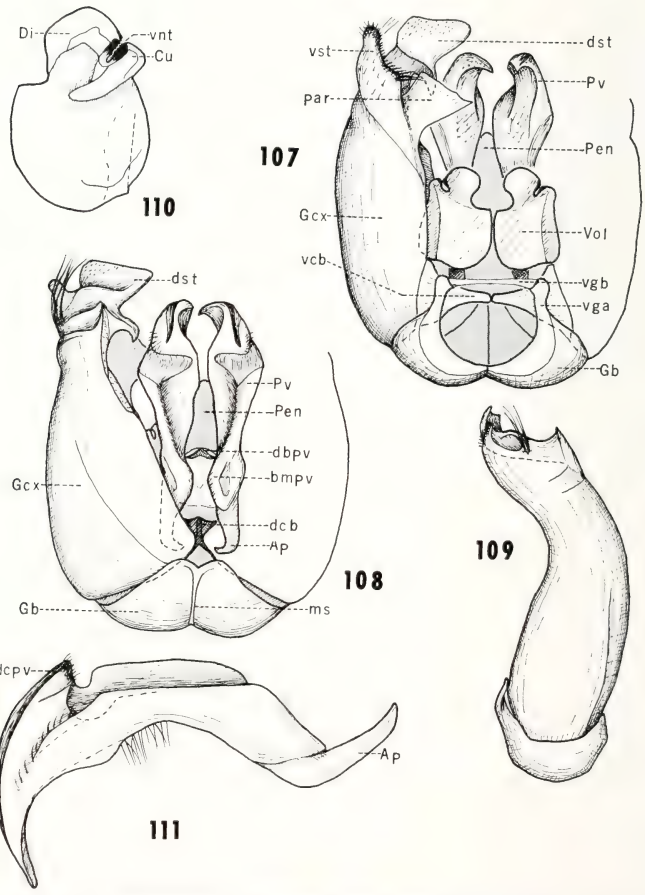




FIGS. **97-100.** Metasoma of *Pseudaugochloropsis graminea* male. **97,** ventral view; **98,** sternum I; **99,** sternum II; **100,** sternum III. **Acs**—acrosternite; **An**—antecosta; **ba**—basal area; **Grd**—gradulus; **ml**—median line.



Figs. **101-106.** Metasomal sterna of *Pseudaugochloropsis graminea* male. **101,** sternum IV; **102,** sternum V; **103,** sternum VI; **104,** sterna VII and VIII fused; **105,** sternum VII; **106,** sternum VIII. **Ap**—sternal apodeme; **Spc**—spiculum.



FIGS. **107-111.** Male genitalia of *Pseudaugochloropsis graminea*. **107,** ventral; **108,** dorsal; **109,** lateral; **110,** volsella, inner view; **111,** penis valve, lateral view. **Ap**—apodeme of penis valve; **bmpv**—basal median projection of penis valve; **Cu**—cuspis; **dbpv**—dorsal bridge of penis valves; **dcb**—dorsal gonocoxal bridge; **dcpv**—dorsal crest of penis valve; **Di**—digitus; **dst**—dorsal process of gonostylus; **Gb**—gonobase; **Gcx**—gonocoxite; **ms**—median sulcus; **par**—ventral parapenial lobe; **Pen**—penis; **Pv**—penis valve; **vcb**—ventral gonocoxal bridge; **vga**—ventral gonobasal arm; **vgb**—ventral gonobasal bridge; **vnt**—volsellar notch; **Vol**—volsella; **vst**—ventral process of gonostylus.

CHARACTERS EMPLOYED

From the almost infinite number of possible characters that might be described and measured on adult halictine bees, I have attempted to select characters for use in the systematic portion of this paper on the following bases: consistency within well-defined genera; discrete differences among well-defined genera; ease of observation on dry specimens; ease of description or illustration; and representation of all major sclerotized external parts and tagmata.

By using several specimens of each exemplar species, some characters could quickly be eliminated on account of excess variability within species. The exemplar study also provided an overall view of many possible characters from which a limited number were selected to be systematically examined in all the species studied. Characters were eliminated or used with qualifications if they appeared to vary more among species in well defined genera than they did between genera.

Measurements were used sparingly, since measurements made on the type species of each genus only, or on only a few species per genus, tend to produce an appearance of quantitative rigor that would not be merited by the few species measured. The benefits to be accrued by standard errors of character states did not appear to justify the work that would have been involved, since adequate numbers of characters whose states differ qualitatively or by large degrees exist to separate genera. In the separation of species in several augochlorine genera, for example, *Augochlora*, a more quantitative approach would be justified and may prove to be absolutely necessary, especially to separate females, but that is beyond the scope of this paper.

Likewise, a number of possibly useful generic characters were excluded because of inaccessibility or difficulty of preparation. A further group of characters appeared to be potentially useful, but were very difficult to describe, an example being the form of the scopa.

While not all characters are equally useful in separating genera, and there is reason to believe that heavily weighting characters from one body tagma or one sex will change a classification (see Michener and Sokal, 1966), there also is no reason to believe that there is a particular set of "magic characters" which one must accurately discern and describe or the classification will be a failure. I make no claims to have found all possible or even all potentially useful characters, but this classification is presented with the belief that use of further characters of adult bees will not radically change the results.

A preliminary study (Eickwort, 1963) showed that many characters which were considered by previous authors, especially those prior to 1930, as existing in discrete qualitative states actually are continuous in their variation when a large number of species is examined. Excessive reliance on one or a few characters led some early authors (notably Schrottky) to unfortunate con-

clusions. For example, wing venation is less reliable than early studies would suggest and small differences in tibial spurs of females are not even reliable to separate species (see Eickwort and Fischer, 1963), although Schrottky used them to separate genera. While some characters used by early authors are utilized here, they are not given special weight.

As mentioned above, there are no ideal characters that *a priori* are totally adequate to separate genera. However, several characters are especially notable for best fitting the criteria outlined in the first paragraph of this section. These are the hidden male metasomal sterna, male genitalia, male metasomal sternum IV, epistomal lobe, distal proboscis structure, and the female hind tibial spur.

However, the classification presented in the next section is based on all the numbered characters listed below. Where one state of a character is found in a majority of genera, it is considered *normal* and so indicated. In the systematic section, characters which are *normal* in state are usually not mentioned at all or are described as being *normal,* the state described below thus indicated.

The female is considered first and all characters comparable in both sexes were measured or described from the female.

FEMALE

Head. (1) **Epistomal sulcus.** The angle formed by the dorsal and lateral clypeo-genal sulci varies from nearly straight (Fig. 112) to acute, in the latter case the epistomal lobe protrudes deeply into the clypeus (Fig. 126). (2) The **clypeus** normally is beveled, with the lower half more coarsely and obscurely punctured and frequently not metallic. Also, normally the clypeus bears two clypeal teeth and a narrow marginal area, as in Fig. 1. Modifications include flattening of the clypeus, projection of the clypeus beyond the marginal area (Fig. 125), and spines (Fig. 115). (3) The **malar area** normally is very short (Fig. 3). In bees with very long heads, the malar area is prolonged (Figs. 136-137). (4) The **preoccipital ridge** varies from rounded to sharply carinate or flanged. (5) **Hypostoma:** The relative length and width of the hypostoma is estimated by measuring the median length (l) of the sclerotized floor of the hypostoma and dividing l by the maximum posterior width (w) of the proboscidial fossa, measured between the hypostomal carinae. These measurements are taken from the head when removed from the body and positioned as in Fig. 4 with the ventral border of the occiput just obscuring the dorsal border. (6) **Hypostomal bridge:** The extent of the hypostomal bridge varies from reaching the posterior margin of the hypostoma to nearly absent. It is estimated by measuring the "closed" length (c) of the hypostomal bridge suture (the stem of the Y) and dividing c by the length of the hypostoma (l), the head positioned as above. (7) **Hypostomal carina:** The anterior angle

is normally rounded; in one genus it is acutely pointed or produced. The posterior flange may be nearly flush with the posterior border of the head, positioned as above, or it may project beyond, as in Fig. 4. (8) The **inner orbit of the compound eye** varies from shallowly to deeply emarginate. The degree of emargination is estimated by positioning the head as in Fig. 1, and measuring the notch width (w) by drawing an imaginary line between the upper and lower inner extremities of the eye and measuring the perpendicular distance from this line to the notch, and dividing w by the total length (l) of the eye. In a few genera, the eyes are enlarged (Figs. 133-134). (9) The **eye hairs** normally are very short, visible only under a microscope; occasionally they are long and conspicuous. (10) The **ocelli** normally are slightly smaller in diameter than the antennal sockets (Fig. 1); occasionally they are enlarged (Fig. 130). (11) **Labrum:** The shape of the basal area is variable, as is the shape of the basal tubercle. Also variable is the shape of the distal process and keel; the keel in one genus is lacking. The labral fimbria are always present but may be placed on the anterior surface of the distal process, in from the lateral margins (Fig. 151). (12) The **mandible** normally bears a subapical tooth and resembles Fig. 11. In some species the mandible is elongate or broadened. The subapical tooth is produced apically in some species so that the mandible appears bidentate at its tip, and the outer posterior ridge may be swollen (Fig. 163). In species of other genera, the mandible bears supplementary teeth (Fig. 162). In one genus, the mandible is sickle shaped (Fig. 168), the subapical tooth lacking, and it resembles the male mandible. (13) The **distal portion of the maxilla** varies considerably in length and width. The length and width of the combined stipes and galea are directly correlated with those of the prementum; only measurements of the prementum are given in the generic descriptions. The anterior conjunctival thickenings normally join the stipes near the base of the distal portion of the maxilla; occasionally the base of the galea is considerably distal to the base of the stipes and the thickenings join the stipes at that point. The apex of the galea is normally rounded and lobed (Fig. 176); in some species it is pointed and well sclerotized (Fig. 20). The inner strip is patterned with cuticular scale-like markings and contains variable numbers of long slender setae besides the few stout short setae which are always present. A *galeal comb* (Fig. 178) consisting of a single row of stout conspicuous setae may be present on the inner surface just below the inner strip; normally it is absent. (14) The **maxillary palpus** varies in length relative to the length of the distal portion of the maxilla, the ratio expressed as the extended length of the palpus (p) to the total length of the galea plus the stipes (M). When the palpus is relatively long, the distal segments are longer and more slender than the basal ones. In one genus, the palpi are greatly elongated (Fig. 182). (15) The **prementum** is normally triangular in cross section and bears two well sclero-

tized *premental thickenings* lining the anterior infolding (Fig. 170). In a few genera, the thickenings are absent and the anterior surface is flattened (Fig. 25). The anterior conjunctival thickenings normally join the prementum near its base; when the thickenings join the stipes far distal to the base of the distal portion of the maxilla, they also join the prementum far beyond its base. The prementum varies considerably in length and width; its length (pl) as measured from base to lateral posterior sclerotized extremities (just basal to the palpi) is estimated relative to the size of the bee by dividing pl by the maximum width of the head (W). The width of the prementum, measured across its distal sclerotized extremities (pw), is estimated relative to its length by dividing pw by pl. (16) The **salivary plate** normally is defined only by a very darkly pigmented U or V shaped brace (Fig. 173), the depth of the V varying with the length of the glossa. In species with a very long glossa, the plate is well sclerotized (Fig. 27) and no conspicuous U or V shaped brace is apparent. (17) The **glossa** varies considerably in length. When fully extended, its length (gl) is estimated relative to the length of the prementum by dividing gl by pl, and relative to the size of the bee by dividing pl by W (width of head). (18) **Labial palpus:** Normally segments 2 plus 3 are longer than 1; occasionally 1 is longer than 2 plus 3, and 1 is flattened in some species.

Mesosoma. (19) **Pronotum:** The dorsal surface is normally concave in lateral view (Fig. 30); in one genus it is convex. The lateral angle varies from rounded to strongly produced (Fig. 188). The dorsal ridge varies from rounded to strongly carinate or lamellate (Fig. 191), as does the lateral ridge. (20) The **mesoscutum** normally is broadly rounded anteriorly and the lip slightly overhangs the pronotum and is rounded (Figs. 30, 32). The mesoscutum may be narrowed anteriorly, and the mesoscutal lip may be produced to strongly overhang the pronotum and be sharply angulate or carinate (Fig. 188). (21) The **tegula** normally is semi-oval in outline (Fig. 34); in one genus its posterior inner angle is produced (Fig. 199). (22) The **basal area of the propodeum** is normally striate or rugose. Occasionally the basal area is sculptured in a fashion characteristic of a genus or species group, or the basal area may be devoid of all striation, being smooth or granular. (23) The **posterior surface of the propodeum** normally resembles Fig. 33, the lateral carinae diverging. The propodeum in some species is narrowed posteriorly, the lateral carinae little diverging. In one genus, the posterior surface is broadened ventrally, the lateral carinae being subparallel. In another genus, the lateral carinae are totally absent. Normally the propodeal pit is narrow although deep (Fig. 33), but it may be enclosed within a V-shaped notch. (24) The **apex of the marginal cell** of the forewing varies from acute (Fig. 201) to truncate and appendiculate (Fig. 37). (25) The **length of the marginal cell,** as measured by the distance from the apex of the stigma to the

apex of the cell (mc), is estimated relative to the length of the wing by dividing mc by the distance from the apex of the stigma to the wing tip (wl). Normally mc wl ranges from .50 to .65; it is greater in cases where the marginal cell is elongate. The **distal hamuli** normally are irregularly spaced (Fig. 39), but in one genus they are very numerous and arranged in one long series. (26) **Tibial spines** at the apex of the hind tibia are normally absent or weakly formed; in some genera they are long and distinct, on the anterior or upper surfaces of the tibia. (27) The inner hind tibial spur, referred to simply as the **hind tibial spur,** has the inner row of serrations variously modified to form teeth or serrations of various forms. In some genera the spur is unmodified and resembles the outer spur. (28) The **scopa** is variously formed and normally present. In one genus it is absent. (29) The **basitibial plate** is narrowly or broadly rounded, well defined on all edges or not; in some genera it is comparatively short or, as in one genus, absent. (30) The **anterior basitarsal brush** may be well-defined, inconspicuous, or apparently absent. When it is absent or very poorly defined, the distal process is not produced.

Metasoma. (31) The **pseudopygidial area** of tergum V is normally clothed with fine, somewhat flattened setae, which may be sparse near the median slit. In some genera, the pseudopygidial area is clothed with darkly pigmented scale-like setae (Fig. 223). In one genus, the pseudopygidial area and the prepygidial fimbria are absent, the tergum resembling that of the male. (32) **Tergum VI** normally resembles Figs. 61 and 62. In some genera, the gradulus is lacking. (33) **Sternum I** is normally unmodified (Fig. 98); in one genus many species bear a median spine or protuberance (Fig. 225). (34) **Sterna IV, V,** and **VI** normally resemble Figs. 67-70. Graduli are normally lacking on sterna IV and V; in some genera they are present. In one genus, sterna IV and V resemble those of the male; in this genus sternum VI bears an unusually well-defined gradulus.

Male

Head. (35) The **antenna** varies in total length and relative lengths of the divisions. The scape (sc) is measured on its upper (longest) surface from the apex of the basal bulb to the tip; flagellomeres 1, 2, 3, and 10 (penultimate) are measured along their midlines (viewed laterally). Normally the antenna does not surpass the end of the mesosoma when extended caudally, and the flagellomeres increase in length progressively towards the apex. Normally the scape is rather long and slender (Fig. 79). When the antenna is very long, the scape is shorter, as in Fig. 181. Its length is measured relative to flagellomere 2 as the ratio sc 2. In some genera, the antenna is lengthened and may surpass the propodeum, and the relative lengths of the flagellomeres are greater when compared with the length of flagellomere 1. Normally the terminal flagellomere is beveled at its apex with the beveled surface shiny

and without setae; in one genus the terminal flagellomere is hooked. Normally the flagellomeres bear sensory plates and setae intermingled; in some species the plates are borne on special *plate areas* that do not bear setae. (36) The **labrum** varies similarly to that of the female, but the basal area always merges gradually into the distal process, and the distal process always lacks a keel.

Mesosoma. (37) The inner **hind tibial spur** is normally unmodified, although some serrations may be inconspicuously enlarged (Fig. 86). In one genus, the spur is pectinate with long teeth.

Metasoma. (38) The shape of the **metasoma** ranges from narrowly oval to quite narrow and elongate; in a few genera, it is petiolate, with the first segment decidedly narrower than the following and sterna I and II very long and narrow (Fig. 237). (39) **Tergum VII** varies in its outline as seen in lateral profile from gradually to abruptly convex and in the presence or absence of a gradulus. (40) **Proctiger:** Tergum VIII and the proctiger of tergum IX vary principally in the form of the anal lip, which may or may not be fringed with post-anal filaments, or otherwise modified. (41) **Sternum III** normally has the apical margin unmodified. Only the postgradular portion, visible without dissection, was systematically examined. In a few genera, the apical margin is modified. (42) **Sternum IV** normally (Fig. 251) is clothed with setae but without distinctive clumps of pubescence, the apical margin not modified, the gradulus either distant from the antecosta or touching it medially, and the antecosta either crossing the bases of the apodemes or not. In many genera, the sternum is modified in a variety of ways. (43) **Sternum V** normally (Fig. 252) resembles the normal state of sternum IV. It may also be modified in a variety of ways, although usually not as strikingly as sternum IV. (44) **Sternum VI** normally resembles Fig. 253, with the gradulus approaching or reaching the antecosta, the apical margin entire or medially notched, and with long strong setae apically on the postgradular area. Modifications usually involve the median postgradular area or the apex. (45) **Sterna VII** and **VIII** are fused laterally and usually dissected as a unit; they are illustrated both joined and separated for most genera. Sternum VII bears lateral apodemes; sternum VIII bears a median spiculum. Modifications of all parts of these sterna are significant generic or specific characters, and the posterior processes are particularly variable. (46) **Gonobase:** The ventral gonobasal bridge varies from membranous to thin and weakly formed to well sclerotized and wide (Fig. 325). The dorsal lobes vary from slight undulations to strong projections. (47) *Gonostylus:* The major variations of the gonoforceps are centered in the gonostyli. Both the ventral and dorsal processes are subject to an almost unlimited range of variation; the ventral process normally bears setae and the dorsal process is frequently membranous, at least in part. A small ventral *basal process* (Fig. 325) is frequently present

at the junction of the gonocoxite and gonostylus below the ventral process, and usually bears setae. (48) Important characteristics of the **penis valves** are the presence and form of a dorsal crest, presence or absence of a *ventral prong* (Fig. 379) or *ventral keel* (Fig. 384), and presence and form of lateral extensions and flanges, and dorsal depressions. The basal median projection and apodeme are relatively invariable. (49) The **volsellae** differ in size relative to the genitalia and the form of the digitus, especially its outline and external ridges.

Not included in the generic descriptions, but mentioned following them, are the general size range and color patterns of the included species. Color and size patterns are seldom strictly adhered to within a large or medium-sized genus, but definite trends become apparent when a long series of species are examined. "Small" bees are usually less than $5\frac{1}{2}$ mm long, "large" bees are longer than about 9 mm, and "medium" sized bees are in between.

Two distinct types of green coloring are present in augochlorine bees, both of which have been called "metallic" by authors. I have reserved the term "metallic" for the rather dull greenish or bluish coloring which characterizes species of *Lasioglossum (Dialictus)* (=*Chloralictus*), the common small sweat bees of North America. The majority of the augochlorine species are not of this color, but rather are much brighter, like most *Augochlora*, *Augochlorella*, and *Augochloropsis;* I refer to this color as "bright" or "brilliant" green (or blue). In some genera (for example, *Neocorynura*), many species are largely black, but bright green tints are usually visible on the head and margins of the mesoscutum.

The characters and their coded states employed in the numerical analysis are listed in Table 1 in Appendix 3. The coding technique is least effective in expressing the qualities of the male genitalia, since homologies of the gonostyli are difficult to ascertain or to code in a logical manner.

SYSTEMATIC TREATMENT

This section is introduced by keys which separate the Augochlorini from other American halictines and distinguish the genera and subgenera of the Augochlorini. The first couplet, distinguishing the Augochlorini, is the most difficult in the keys to use; a companion paper (Eickwort, in preparation) will more completely characterize the tribe.

The sexes are treated separately in the keys. As nearly as possible, only externally visible characters are used and the keys are therefore somewhat artificial. Males are more difficult than females to identify without dissection, since they usually lack such useful "key" characters as modified tibial spurs and basitibial plates; when in doubt, the genitalia should be compared with the figures.

KEYS TO GENERA AND SUBGENERA OF THE AUGOCHLORINI

Subfamily Halictinae

Females

Pseudopygidial area of metasomal tergum V slit medially; if pseudopygidial area absent, integument bright green and coarsely punctate; without scopa; outer veins of forewing always strong ..... Tribe Augochlorini

Pseudopygidial area entire; if area absent, integument not bright green; outer veins of forewing either strong or weakened ..... other Halictinae

Males

Pygidial plate of metasomal tergum VII absent; posterior margin of tergum VII not bent anteriorly; apex of metasomal sternum VIII with median spiculum ..... Tribe Augochlorini

Pygidial plate defined, at least on posterior margin; posterior margin of tergum VII bent anteriorly, thus visible in ventral view of bee; sternum VIII without spiculum ..... other Halictinae

Tribe Augochlorini

Females

1. Mouthparts very long and slender, as in Figs. 171 and 182; clypeus and supraclypeal area strongly produced (Figs. 129, 132); epistomal sulcus forming right angle 2

   Mouthparts not very long and slender; clypeus and supraclypeal area not strongly produced; epistomal sulcus variable 5

2(1). Maxillary palpi greatly lengthened (Fig. 182), reaching metasoma when mouthparts retracted into proboscidial fossa ..... *Ariphanarthra*

   Maxillary palpi not greatly lengthened 3

3(2). Eyes greatly enlarged, projecting above vertex and nearly reaching enlarged lateral ocelli and subantennal sulci (Fig. 130); basitibial plate not short, much surpassing apex of femur .... *Megaloptidia*

   Eyes not projecting above vertex; ocelli enlarged or not; basitibial plate very short, little surpassing apex of femur ..... *Megommation s. l.* 4

4(3). Ocelli enlarged (Fig. 128); hind tibial spur serrate ..... *Megommation (Megommation)*

   Ocelli not enlarged; hind tibial spur pectinate (Fig. 218) ..... *Megommation (Megaloptina)*

5(1). Hind tibial spur serrate, teeth shorter than wide, pointed or rounded 6

   Hind tibial spur pectinate, teeth longer than wide 14

6(5). Scopa and pseudopygidial area absent, integument coarsely punctate ..... *Temnosoma*

   Scopa and pseudopygidial area present 7

7(6). Hind tibial spur with rounded serrations (Figs. 214-216); preoccipital ridge sharply angled or carinate; epistomal sulcus variable 8

   Hind tibial spur with sharp serrations, as on outer spur, or with short narrow teeth (Figs. 206-207); preoccipital ridge sharply angled or rounded; epistomal sulcus forming obtuse angle 13

8(7). Epistomal sulcus forming acute angle, epistomal lobe protruding onto clypeus (Figs. 125-126); clypeus relatively flat, green almost to apex; anterior angle of hypostomal carina usually a sharp right angle or produced into spine; marginal cell truncate and usually appendiculate ..... *Augochlora s. l.* 9

Epistomal sulcus forming obtuse or right angle; clypeus beveled, area below angle not green; anterior angle of hypostomal carina rounded; marginal cell acute or very narrowly truncate 11

9(8). Mandible normal, subapical tooth not produced; pseudopygidial area of tergum V with long setae, not scale-like; sternum I usually normal, rarely with slight median ridge or tooth; basitibial plate usually narrowly rounded, occasionally broadly rounded; basal elevation of labrum suborbicular ..... *Augochlora (Oxystoglossella)*

Mandible bidentate (Fig. 163), subapical tooth and occasionally outer posterior ridge produced; pseudopygidial area of tergum V with scale-like setae (Fig. 223); sternum I frequently toothed or with median ridge, may be unarmed; basitibial plate broadly rounded; basal elevation of labrum transverse 10

10(9). Apex of clypeus prolonged beyond marginal area, rounded and slightly upturned, concealing half of labral basal area (Fig. 125) ..... *Augochlora (Mycterochlora)*

Apex of clypeus normal, not produced (Fig. 126) ..... *Augochlora (Augochlora)*

11(8). Epistomal sulcus forming obtuse angle (Fig. 124); hind tibial spur with basal area not raised (Fig. 215); basitibial plate poorly defined on anterior edge; preoccipital ridge carinate ..... *Ceratalictus*

Epistomal sulcus forming right or slightly obtuse angle; hind tibial spur with basal area raised (Fig. 214) or basal tooth high (Fig. 216); basitibial plate well defined on all edges; preoccipital ridge sharply angled or carinate 12

12(11). Hind tibial spur with few short rounded teeth, basal tooth largest (Fig. 216); basal area of propodeum striate basally, strongly granular; labrum as in Fig. 158; size small (about 5 mm) ..... *Pereirapis*

Hind tibial spur with rounded serrations, basal area raised, as in Fig. 214; basal area of propodeum not strongly granular; labrum usually as in Fig. 157, rarely as in *Pereirapis*; size usually larger than 5 mm ..... *Augochlorella*

13(7). Basal area of propodeum completely smooth or granular, no striae; preoccipital ridge gradually rounded; eyes deeply emarginate (Fig. 112) ..... *Corynura (Corynura)*

Basal area of propodeum roughened or with weak plicae basally; preoccipital ridge sharply angled; eyes moderately emarginate (Fig. 120) ..... *Paroxystoglossa*

14(5). Malar area as long as wide or longer; head greatly elongate 15

Malar area much shorter than wide; head not greatly elongate 16

15(14). Pronotum (Fig. 198) convex dorsally, lateral angle and lateral ridge absent; epistomal sulcus forming acute angle (Fig. 135); scutellum normal ..... *Chlerogella*

Pronotum normal; epistomal sulcus forming right angle (Figs. 136-137); scutellum produced into two large tubercles (?) ..... *Chlerogas**

16(14). Eyes and ocelli usually enlarged (Figs. 133-134); epistomal sulcus acutely angled, forming deep lobe; labrum and mandibles as in Figs. 159, 161 and 162 ..... *Megalopta*

Eyes and ocelli not enlarged; epistomal sulcus variously angled, not forming deep lobe; labrum and mandibles not as above 17

17(16). Tegula with inner posterior angle produced (Fig. 199); pronotal dorsal ridge lamellate, forming flange from lateral angle to lobe (Fig. 189); basitibial plate very short, extending barely past apex of femur (Fig. 204); labrum with distal process expanded and rounded, distal keel projecting beyond apex (Fig. 151) ..... *Augochloropsis s. l.* 18

Tegula not produced; pronotal dorsal ridge variable; basitibial plate not short, except in *Corynura (Callochlora);* labrum not as above, may be expanded distally 19

18(17). Basal area of propodeum deeply and regularly pitted or strongly striate basally, smooth apically ..... *Augochloropsis (Augochloropsis)*

Basal area of propodeum not as above, smooth, irregularly roughened, or with light plicae ..... *Augochloropsis (Paraugochloropsis)*

19(17). Pronotal dorsal ridge lamellate, forming flange from lateral angle to pronotal lobe; mesoscutum strongly produced over pronotum, usually forming carinate or lamellate flange 20

Pronotal dorsal ridge not lamellate; mesoscutum variable 21

20(19). Vertex swollen behind ocelli, clypeus usually armed with spines or median tubercle (Figs. 114-116); basal area of propodeum smooth, usually depressed transversely, bare; base of metasomal tergum I normal ..... *Rhinocorynura*

Vertex not swollen, clypeus not armed; basal area of propodeum short, striate, completely covered with short dense pile; tergum I with basal enclosure formed by dense plumose hairs near petiole, usually containing large mites ..... *Thectochlora*

21(19). Pronotal lateral angle produced, strongly carinate anteriorly and laterally; dorsal ridge not carinate behind lateral angle (Figs. 184-185); lateral ridge carinate; mesoscutum slightly produced over pronotum, low and sharply angled; preoccipital ridge rounded 22

Pronotal lateral angle not strongly carinate anteriorly; if produced, dorsal ridge carinate; lateral ridge variable; mesoscutum and preoccipital ridge variable 23

22(21). Marginal cell of forewing very long, extending about 4/5 distance from apex of stigma to apex of wing; stigma enlarged; pronotum as in Fig. 184 ..... *Corynurella*

Marginal cell of forewing of normal length, extending about 3/5 distance from apex of stigma to apex of wing; stigma not enlarged; pronotum as in Fig. 185 ..... *Rhectomia*

* The female is unknown. Characters hypothesized from males.

23(21). Epistomal sulcus forming right or slightly acute angle 24
Epistomal sulcus forming obtuse angle 27

24(23). Preoccipital ridge rounded, vertex produced to rounded ridge above ocelli (Figs. 1, 3); galea of maxilla with apex pointed, well-sclerotized (Fig. 21); basal elevation of labrum with apical surface flattened, rimmed (Figs. 7-8) ..... *Pseudaugochloropsis*
Preoccipital ridge sharply angled or carinate, vertex not produced; galea normal, with apical lobe; labrum not as described above 25

25(24). Basitibial plate well-defined posteriorly, obsolescent anteriorly (Fig. 203); hind tibial spur with few teeth (Fig. 212); pronotal lateral angle not produced, forming obtuse angle; eye hair short; restricted to Andean region ..... *Andinaugochlora*
Basitibial plate well-defined on all edges *or* tibial spur closely pectinate; pronotal lateral angle frequently produced, occasionally obtuse; eye hair frequently long; widespread ..... *Caenaugochlora s. l.* 26

26(25). Basitibial plate well-defined on all edges; tibial spur not closely pectinate; eye hair frequently long ..... *Caenaugochlora (Caenaugochlora)*
Basitibial plate obsolescent anteriorly; tibial spur closely pectinate, over 10 teeth (Fig. 217); eye hair short ..... *Caenaugochlora (Ctenaugochlora)*

27(23). Preoccipital ridge carinate or lamellate; mesoscutum *usually* narrowed anteriorly and mesoscutal lip *usually* narrow, high, projecting forward and sharply angled (Fig. 187); pronotal lateral angle *usually* strongly produced, lateral ridge carinate or lamellate; propodeum *usually* narrowed posteriorly, lateral carinae little diverging ..... *Neocorynura s. l.* 28
Preoccipital ridge rounded; mesoscutum not narrowed anteriorly, mesoscutal lip *usually* not high or narrow, pronotal lateral angle *usually* not produced; pronotal lateral ridge sharply angled or rounded; propodeum not narrowed posteriorly 29

28(27). Preoccipital ridge strongly lamellate, flange recurving over gena; pronotal lateral ridge strongly lamellate; known from Bolivia and Peru ..... *Neocorynura (Neocorynuroides)*
Preoccipital ridge and pronotal lateral ridge carinate; widespread ..... *Neocorynura (Neocorynura)*

29(27). Head, mesosoma and metasoma brilliant green or orange-green; propodeal basal area weakly striate 30
Head and mesosoma dull metallic green or blue, black or brownish; metasoma variously colored but not brilliant green; propodeal basal area smooth or roughened 31

30(29). Eyes with long hair; basitibial plate (Fig. 202) defined only posteriorly, very short ..... *Corynura (Callochlora)*
Eyes with short hair; basitibial plate well-defined on all edges, of normal length ..... *Augochlorodes*

31(30). Basal area of propodeum roughened; bee dull metallic; size small (5-6 mm) ..... *Halictillus*
Basal area of propodeum smooth or granular; bee variously colored, size usually larger than 6 mm ..... *Corynura (Corynura)*

Males

1. Mouthparts very long and slender, as in Figs. 171 and 182; clypeus and supraclypeal area strongly produced (Figs. 129, 132); epistomal sulcus forming right angle 2
Mouthparts not very long and slender; clypeus and supraclypeal area not strongly produced; epistomal sulcus variable 5

2(1). Maxillary palpi greatly lengthened (Fig. 182), reaching metasoma when mouthparts retracted into proboscidial fossa ..... *Ariphanarthra*
Maxillary palpi not greatly lengthened 3

3(2). Eyes greatly enlarged, projecting above vertex and nearly reaching enlarged lateral ocelli and subantennal sulci (Fig. 130); metasomal sternum IV bilobed with deep median notch, lobes strongly pilose ..... *Megaloptidia*
Eyes not projecting above vertex; ocelli enlarged or not; metasomal sternum IV not bilobed, with row or rows of strong modified setae laterally bordering gradulus (Figs. 262-263) ..... *Megommation s. l.* 4

4(3). Ocelli enlarged (Fig. 128); propodeum without dense patches of pubescence; metasomal sternum V strongly emarginate ..... *Megommation (Megommation)*
Ocelli not enlarged; lateral surfaces of propodeum with patches of dense pubescence near spiracles; metasomal sternum V weakly emarginate ..... *Megommation (Megaloptina)*

5(1). Malar area as long as wide or longer; head greatly elongate 6
Malar area much shorter than wide; head not greatly elongate 7

6(5). Pronotum (Fig. 198) convex dorsally, lateral angle and lateral ridge absent; epistomal sulcus forming acute angle; scutellum normal (?) ..... *Chlerogella**
Pronotum normal; epistomal sulcus forming right angle (Figs. 136-137); scutellum produced into two large tubercles .. *Chlerogas*

7(5). Tegula with inner posterior angle produced (Fig. 199); pronotal dorsal ridge lamellate, forming flange from lateral angle to lobe (Fig. 189); metasomal sternum IV with lateral appendages, usually hidden or partly projecting from beneath tergum IV, sternum posteriorly emarginate with median point (Figs. 243-244) [lateral appendages nearly absent in a few species (Fig. 245)]; posterior margins of metasomal terga I and II frequently each with a row of strong setae (Fig. 224); marginal cell of forewing truncate ..... *Augochloropsis s. l.* 8
Tegula not produced; pronotal dorsal ridge variable; metasomal sternum IV variable; posterior margins of metasomal terga without rows of strong setae; marginal cell of forewing variable 9

8(7). Metasomal sternum V with apical margin notched, centrally with long curved setae; sternum VI with wide apical flanges projecting beyond posterior border (Fig. 246); distal process of labrum truncate or notched apically; ventral gonostylus bearing row of strong, flattened, modified setae at apex (Figs. 362-363) ..... *Augochloropsis (Augochloropsis)*

* The male is unknown. Characters hypothesized from female.

Metasomal sternum V with apical margin entire, setae not modified; sternum VI with apical flanges little developed (Fig. 247); distal process of labrum rounded (Fig. 152); ventral gonostylus bearing dense unmodified setae at apex (Fig. 366) ..... *Augochloropsis (Paraugochloropsis)*

9(7). Metasomal sternum IV with conspicuous apical or median tufts of specialized setae or strong cuticular ridges and depressions 10

Metasomal sternum IV usually not modified; apical margin at most emarginate or with posterior lateral projections (Figs. 248-249), usually hidden 15

10(9). Eyes and ocelli usually enlarged (Fig. 133); metasomal sternum III bilobed (Fig. 264); sternum IV with posterior margin notched laterally, bilobed medially, and with median flap (Fig. 265); pronotal dorsal ridge (Figs. 195-196) rounded and narrow, anterior edge of lateral angle and lateral ridge carinate ..... *Megalopta*

Eyes and ocelli not enlarged; metasomal sternum III not strongly bilobed, may be medially emarginate; sternum IV not as above; pronotal dorsal ridge carinate or lamellate, lateral angle not strongly carinate on anterior margin, lateral ridge variable 11

11(10). Pronotal dorsal ridge and mesoscutal lip lamellate, forming flange (Fig. 191); antenna long, scape less than 1.5 times length of flagellomere 2; metasomal sternum IV (Fig. 249) produced into caudally directed processes which bear strong setae (usually hidden), posterior margin depressed and truncate, median patch of short erect stout setae; sternum V emarginate, with long plumose pubescence ..... *Thectochlora*

Pronotum and mesoscutum not lamellate; antenna of variable length, scape more than 1.5 times length of flagellomere 2; metasomal sterna IV and V not as above 12

12(11). Epistomal sulcus forming obtuse angle; metasomal sternum IV without distinctive median or posterior setal patches, with posterior margin emarginate and centrally depressed and shiny, or with shiny median apical depression bordered by sharp ridges (Fig. 238); sternum V with median shiny depression usually bordered by strong ridges (Fig. 239) ..... *Paroxystoglossa*

Epistomal sulcus forming right angle; metasomal sternum IV with distinctive median or apical setal patches; sternum V variable 13

13(12). Terminal antennal flagellomere hooked (Fig. 79); preoccipital ridge rounded ..... *Pseudaugochloropsis*

Terminal antennal flagellomere not hooked; preoccipital ridge sharply angled or carinate ..... *Caenaugochlora s. l.* 14

14(13). Metasomal sternum IV (Fig. 256) bearing distinctive setal clumps on raised tubercles to either side of apical median depression; eyes often bear long hairs ..... *Caenaugochlora (Caenaugochlora)*

Metasomal sternum IV (Fig. 257) with V-shaped patch of setae bordering slight median depression, eyes with short hairs ..... *Caenaugochlora (Ctenaugochlora)*

15(9). Body very coarsely punctate; metasomal terga I to III strongly depressed basally; antenna short, as in Fig. 180; metasomal tergum VII prolonged apically and bilobed (Figs. 230-231) ..... *Temnosoma*

Body not very coarsely punctate; metasomal terga not strongly depressed; antenna not as in Fig. 180, length variable; metasomal tergum VII not prolonged or bilobed 16

16(15). Pronotal dorsal ridge lamellate, forming flange from lateral angle to lobe (Figs. 186, 191); mesoscutum strongly produced over pronotum, lip usually carinate or lamellate 17

Pronotal dorsal ridge not lamellate and forming flange, mesoscutum variable but lip not carinate or lamellate 18

17(16). Vertex swollen above ocelli; basal area of propodeum smooth; metasomal sterna IV and V unmodified; scape more than twice length of flagellomere 2 ..... *Rhinocorynura*

Vertex not swollen; basal area of propodeum striate; metasomal sternum IV (Fig. 249) produced into caudally directed processes bearing strong setae (usually hidden), posterior margin depressed and truncate, median patch of short erect stout setae; sternum V emarginate, with long plumose pubescence; scape less than 1.5 times as long as flagellomere 2 ..... *Thectochlora*

18(16). Antenna very long, scape usually shorter than flagellomere 2, never more than 1.25 times length of 2; flagellomere 2 usually subequal to or longer than 10; preoccipital ridge rounded 19

Antenna of variable length, but scape over 1.25 times length of flagellomere 2; flagellomere 2 usually shorter than 10; preoccipital ridge variable 21

19(18). Metasoma elongate, not petiolate; size small (about 5-6 mm); color metallic blue-green; genitalia as in Figs. 331 to 334 ..... *Halictillus*

Metasoma petiolate, segments I and II long and narrow, as in Fig. 237; if not, color usually bright green or orange-green; size usually larger than 6 mm; genitalia as in Figs. 325 to 330 ..... *Corynura s. l.* 20

20(19). Integument bright green or orange-green; hairs on eyes long; metasoma elongate but not distinctly petiolate ..... *Corynura (Callochlora)*

Integument not bright green; mesosoma dull metallic, black, or brown; hairs on eyes short; metasoma usually distinctly petiolate ..... *Corynura (Corynura)*

21(18). Pronotal lateral angle produced and strongly carinate anteriorly and laterally (Figs. 184-185), dorsal ridge posterior to lateral angle not carinate, lateral ridge carinate; mesoscutum slightly produced over pronotum, low and sharply angled; preoccipital ridge rounded 22

Pronotal lateral angle not strongly carinate anteriorly, if produced, dorsal ridge carinate, lateral ridge variable; mesoscutum and preoccipital ridge variable 23

22(21). Marginal cell of forewing very long, extending about 0.8 distance from apex of stigma to apex of wing; stigma enlarged; pronotum as in Fig. 184 ..... *Corynurella*

Marginal cell of forewing normal, extending about 0.6 distance from apex of stigma to apex of wing; stigma not enlarged; pronotum as in Fig. 185 ..... *Rhectomia**

23(21). Preoccipital ridge rounded; metasomal sternum IV (Fig. 248) emarginate with lateral process bearing low setae, processes usually hidden by tergum IV with setae protruding from beneath apical margin of tergum; inner hind tibial spur with long serrations; body shiny green, weakly punctate; basal area of propodeum smooth with fine short basal plicae; known only from southern Brazil ..... *Augochlorodes*

Preoccipital ridge sharply angled or carinate; metasomal sternum IV not as above; inner hind tibial spur normal, with short serrations; body variously colored and punctured 24

24(23). Epistomal sulcus forming obtuse angle 25

Epistomal sulcus forming acute or right angle 28

25(24). Antenna reaching about to scutellum, scape more than 2.5 times length of flagellomere 2, 2 subequal to 1; mesoscutum not narrowed and not produced over pronotum; integument bright green, tibiae and tarsi orange. (Compare with *Augochlorella* and *Pereirapis*.) ..... *Ceratalictus*

Antenna long, frequently surpassing propodeum, scape less than 2.5 times length of flagellomere 2, 2 longer than 1 and usually more than 1.5 times length of 1; mesoscutum usually narrowed and produced over pronotum; color variable 26

26(25). Metasomal sterna IV and V depressed medially and shiny; posterior margin of IV broadly emarginate; venter of head and mesosoma and lower surfaces of legs clothed with long plumose pubescence; metasoma not petiolate; known from southern Brazil to Argentina ..... *Paroxystoglossa*

Metasomal sterna IV and V not modified; venter without long plumose pubescence; metasoma frequently petiolate (Fig. 222); sterna I and II usually very long and narrow (Fig. 237); widespread. (Compare with *Andinaugochlora*.) ..... *Neocorynura s. l.* 27

27(26). Preoccipital ridge and lateral ridge of pronotum carinate, not strongly lamellate; widespread ..... *Neocorynura (Neocorynura)*

Preoccipital ridge lamellate, flange recurving over gena; lateral ridge of pronotum strongly lamellate; known from Bolivia and Peru ..... *Neocorynura (Neocorynuroides)*

28(24). Antenna very long, surpassing propodeum; scape twice or less times length of flagellomere 2; flagellum with plate areas containing only sensory plate-organs, these areas without setae; metasomal sternum VI (Fig. 241) strongly notched with deep concavities to either side of median notch; restricted to Andean region. (Compare with *Neocorynura*) ..... *Andinaugochlora*

* Not known from male sex. Characters hypothesized from female.

Antenna of moderate length, usually not surpassing propodeum; scape over 3 times length of flagellomere 2, flagellum without specialized plate areas (antenna rarely long and with plate areas in *Augochlora*); metasomal sternum VI without deep concavities to either side of median notch; widespread 29

29(28). Epistomal sulcus forming acute angle, epistomal lobe protruding into clypeus; marginal cell of forewing truncate, usually appendiculate ..... *Augochlora s. l.* 30

Epistomal sulcus forming right angle; marginal cell of forewing acute, rarely narrowly truncate. (Compare with *Ceratalictus.*) 32

30(29). Metasomal sterna V and VI with strong median apical depressions, bordered by stiff setae on VI and by median ridge at base of depression on V; posterior margin of tergum VII flanged outwards, appearing carinate .... *Augochlora (Mycterochlora)*

Metasomal sterna V and VI and tergum VII not modified, not as described above 31

31(30). Lateral ridge bordering ventral gonostylus (Fig. 377) with short setae ..... *Augochlora (Augochlora)*

Lateral ridge bordering ventral gonostylus (Fig. 381) with long setae, surpassing gonostylus ..... *Augochlora (Oxystoglossella)*

32(29). Metasomal sternum IV broadly emarginate posteriorly, laterally bearing long modified setae which are usually hidden (Fig. 254); size small, about 5 mm; genitalia as in Figs. 393-396 ..... *Pereirapis*

Metasomal sternum IV not broadly emarginate, without long lateral setae; size usually larger than 5 mm; genitalia (Figs. 384-387) with inner lobe of ventral gonostylus bearing marginal row of flattened setae ..... *Augochlorella*

Genus **Corynura** Spinola

Female

HEAD. (Fig. 112). (1) Epistomal sulcus forming obtuse angle. (4) *Preoccipital ridge gradually rounded.* (5, 6) *Hypostomal floor very short and broad, width subequal to or greater than length,* l/w = .63 to 1.04, c/l = 0 to .59 (7 spp.). (7) Posterior flange projects beyond occiput. (8) Inner orbit of compound eye strongly emarginate, w/l = .127 to .158 (7 spp.)*. (11) Labrum (Figs. 139-140) with distal process broadly triangular, usually as wide as and as long as or longer than basal area. Basal elevation usually rounded and transverse, strongly protuberant. Distal keel normal or flattened apically (Fig. 140). (13) *Distal portion of maxilla short and broad* (Fig. 177), *with base of galea far distal to base of stipes, at junction of anterior conjunctival thickenings. Well-formed galeal comb present* (Fig. 178). Inner strip with broad scale-like cuticular markings, no long setae. (14) Maxillary palpus p/M = .42 to .64 (11 spp.). (15) Prementum normal (Fig. 169) with anterior conjunctival thickenings far distal to its base, pl/W = .50 to .61, pw/pl = .24 to .32 (11 spp.). (16) Salivary plate normal, broad U-shaped

brace (Fig. 173). (17) *Glossa short*, gl pl = .28 to .41, gl W = .16 to .24 (11 spp.).

MESOSOMA. (19) Pronotal dorsal ridge carinate, often weakly so. Lateral angle usually not produced, obtuse, occasionally produced to an acute angle (Fig. 183). Lateral ridge rounded, sharp when lateral angle produced. (20) Mesoscutum not narrowed anteriorly, lip rounded*. (23) Propodeal pit enclosed within V-shaped notch arising at junction with posterior marginal area. (24, 25) Marginal cell of forewing acute, mc wl = .55 to .63 (6 spp.). (26) Long tibial spine or spines present. (30) Anterior basitarsal brush well-defined.

METASOMA. (31) Tergum V may bear short acrotergite above antecosta. Sterna and terga otherwise normal*.

Male

HEAD. (35) *Antenna* (Fig. 183) *very long, scape shorter than or subequal to flagellomere 2, 2 longer than 10**; sc 2 = .79 to 1.18, 2 1 = 2.31 to 3.25, 3 1 = 2.28 to 3.14, 10 1 = 2.14 to 2.86 (5 spp.). Plate areas usually present, rarely absent. (36) Labrum (Fig. 142) short and transverse, distal process absent or nearly so, basal elevation extending across basal area, not notched.

METASOMA. (38) *Metasoma long, narrow, and petiolate, sterna I and II very long and narrow*, similar to *Neocorynura* (Fig. 237). (39) Tergum VII gradually convex apically, gradulus absent or weakly defined. (40) Anal lip of proctiger without post-anal filaments. (42-44) Sterna IV to VI normal, apex of VI weakly notched. (45) Posterior margins of sterna VII and VIII (Figs. 268-273) usually variously produced medially, usually bearing setae. Sternum VIII joins VII laterally at apices of apodemes. Spiculum broad. (46) Gonobase (Figs. 325-330) with broad ventral bridge, dorsal lobes weakly formed. (47) Ventral gonostylus projecting from strong lateral ridge, seta-bearing surface directed cephalad and scarcely visible from ventral view, additional ventrally facing seta-bearing surface more or less developed. Basal process of gonostylus present. Dorsal gonostylus a simple ridge. (48) Penis valve (Fig. 327) without dorsal crest, with slight ventral keel, medial edge slightly expanded, with longitudinal dorsal groove. (49) Volsella (Fig. 328) with inner posterior angle variously produced.

*Exceptions

In two species with broad heads, the eyes are less emarginate, w/l = .096 to .107. In *Corynura chilensis* (Spinola), which has strongly protuberant pronotal lateral angles (Fig. 183), the mesoscutal lip is high, although the mesoscutum is not narrowed anteriorly. In two species examined, the pseudopygidial area bears scale-like setae bordering the median slit. In *Corynura (Callochlora) prothysteres* (Vachal), flagellomere 2 is shorter than 10, 2 1 =

1.31, 3/1 = 1.53, and 10/1 = 2.44, although the antennae are very long and bear plate areas.

Corynura is a moderate-sized genus of Chilean and Argentinian bees, with a few species reaching southern Brazil and Bolivia. It is composed of two subgenera, appearing quite different at first glance but quite similar in most generic characters.

Subgenus **Corynura** Spinola

Corynura Spinola, 1851, Historia fisica y politica de Chile, Zoologia, 6:296. (Type species: *Corynura gayi* Spinola, 1851, designated by Alfken, 1926).

Corynogaster Sichel, 1867, Hymenoptera Fossoria et Mellifera. Supplement to H. de Saussure, Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. vol. 2: Hymenoptera:146. *lapsus* for *Corynura*?

Rhopalictus Sichel, 1867, Hymenoptera Fossoria et Mellifera. Supplement to H. de Saussure, Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. vol. 2: Hymenoptera:146. (Type species: *Corynura flavofasciata* Spinola, 1851, designated by Alfken, 1926).

Female

(9) Compound eye with hairs of normal length. (22) Basal area of propodeum completely smooth or granular, no striae. (27) Hind tibial spur usually with sharp serrations (Fig. 206) as on outer spur or pectinate with short teeth (Fig. 207), rarely with long teeth. (29) Basitibial plate well-defined on all edges, narrowly rounded.

Male

(47) Basal process of gonostylus with setae.

Species of *Corynura s. s.* are black or dull metallic bees, occasionally with a red metasoma, never bright green, small to medium sized. The long petiolate abdomen and very long antennae of the male distinguish *Corynura* from all other halictines within its range except *Neocorynura,* which has a carinate preoccipital ridge and antennae with the scape longer than flagellomere 2. Females of *Corynura* resemble species of *Halictus* or *Lasioglossum s. l.* more than they do most augochlorine genera, due to their color. They are most likely to be confused with *Ruizantheda,* a relative of *Agapostemon* with long-haired compound eyes and tibial spurs with lamellate teeth.

Corynura was the first described augochlorine genus. Spinola (1851) named two species, *Corynura gayi* and *C. flavofasciata,* from a wasp female and halictine males and placed the genus near the Thynnidae. However, the generic description dealt primarily with the males and the name has usually been used for bees. Sichel (1867) correctly associated a halictine female with the male of *C. flavofasciata* and named *Rhopalictus* for the halictines in Spinola's *Corynura,* assuming that *Corynura* should be reserved for wasps. He mistakenly used *Corynogaster* instead of *Corynura* to refer to Spinola's genus, and did not intend to create a genus by that name, as pointed out by Herbst (1917).

Until recently, *Corynura* was used also to refer to species correctly placed in *Neocorynura*. Alfken (1926) published a revision of the Chilean *Corynura* and an extensive discussion and historical summary of the genus. He quite clearly recognized that *Corynura* is distinct from species now placed in *Neocorynura*, but unfortunately placed *Corynura chilensis* (Spinola) (= *C. flavofasciata* Spinola), the type species of *Rhopalictus*, with the latter group and consequently called this group *Rhopalictus* instead of *Neocorynura*, which he considered a synonym of *Rhopalictus*. Alfken later (1931) published a correction to his description of *Corynura* and a revised key to the species.

Sandhouse (1943) mistakenly thought that *Corynura* was described as a subgenus of *Halictus* by Spinola and designated *Halictus gayi* Spinola as type species for *Corynura*, *Corynogaster*, and *Manuelia*. The former two designations are invalid since *Corynura gayi* Spinola, not *Halictus gayi* Spinola, was included in *Corynura* by Spinola. *Halictus gayi* is a ceratinine bee, to which *Manuelia* correctly refers (Vachal, 1905).

Moure (1944a) listed the complete synonymy of *Corynura*, including all citations of species of *Corynura*, and eliminated those referring to species of *Neocorynura*.

Well known species of *Corynura s. s.* include *C. chilensis* (Spinola), *C. corynogaster* (Spinola), and *C. rubella* (Haliday).

Subgenus **Callochlora** Moure, new status

Callochlora Moure, 1964, J. Kansas Entomol. Soc. 37:269. (Type species: *Halictus chloris* Spinola, 1851, original designation).

Female

(9) *Compound eyes with long hair.* (22) Basal area of propodeum with striae. (27) Hind tibial spur (Fig. 208) pectinate, with long teeth. (29) Basitibial plate (Fig. 202) defined only posteriorly, very short.

Male

(47) Basal process of gonostylus without setae (Fig. 329).

Species of *Callochlora* are bright green or bright coppery green and thus appear quite different from *Corynura s. s.* The male metasoma is elongate but not so distinctly petiolate as in *Corynura s. s.* The long-haired eyes and obtuse epistomal lobes distinguish its species from other bright green augochlorine bees.

Moure (1964) described *Callochlora* for two species, *C. chloris* (Spinola) and *C. prothysteres* (Vachal). He illustrated the genitalia of *C. chloris*, but reversed the captions for it and *Ruizantheda*. Figure 3 of Moure (1964), labeled *C. chloris*, actually illustrates the genitalia of *R. proxima* (Spinola) while Fig. 2 actually illustrates *C. chloris*; Fig. 1, labeled *R. proxima*, actually illustrates *R. mutabilis* (Spinola).

Genus **Halictillus** Moure

Halictillus Moure, 1947, Publ. avulsas Mus. paranaense no. 3:7. (Type species: *Chloralictus loureiroi* Moure, 1941, monobasic and original designation.)

Female

HEAD (Fig. 113). (1) Epistomal sulcus forming obtuse angle. (4) Preoccipital ridge rounded. (5, 6) Hypostomal floor slightly longer than wide, l/w = 1.07 to 1.16, c/l = .25 to .26 (2 spp.). (8) Inner orbit of compound eye moderately emarginate, w/l = .085 to .097 (3 spp.). (11) Labrum (Fig. 141) with distal process narrowly triangular, sometimes protruding just below basal area to lateral margins of basal area; basal elevation suborbicular, rounded and protuberant. (13) *Distal portion of maxilla with base of galea far distal to base of stipes, at junction of anterior conjunctival thickenings,* as in *Corynura* but longer and narrower. *Galea comb present, of 6 or more teeth,* inner strip with broad scale-like markings, no long setae. (14) Maxillary palpus long, p/M = .41 to .50 (3 spp.). (15) Prementum as in *Corynura,* anterior conjunctival thickenings joining prementum far distal to its base, pl/W = .56 to .70, pw/pl = .21 to .25 (3 spp.). (16) Salivary plate normal. (17) Glossa rather short, less than half length of prementum, gl/pl = .31 to .44, gl/w = .20 to .31 (3 spp.).

MESOSOMA. (19) Pronotal lateral angle obtuse, not produced; dorsal ridge carinate, lateral ridge rounded. (20) Mesoscutum not narrowed anteriorly, lip rounded. (22) Basal area of propodeum roughened, posterior edge smooth or granular. (23) Propodeal pit enclosed within V-shaped notch arising at junction with posterior marginal area. (24, 25) Marginal cell acute, mc/wl = .47 to .57 (2 spp.). (26) Long tibial spines present. (27) *Hind tibial spur* (Fig. 209) *pectinate, all teeth long.* (29) Basitibial plate poorly defined on anterior edge, well defined posteriorly, narrowly rounded. (30) Anterior basitarsal brush well-defined.

Male

HEAD. (35) *Antenna very long, surpassing propodeum, plate areas present, scape shorter than or subequal to flagellomere 2, 2 longer than 10, as in Corynura:* sc/2 = .90 to .91, 2/1 = 2.75 to 3.70, 3/1 = 2.38 to 3.33, 10/1 = 2.18 to 3.03 (2 spp.). (36) Labrum short and transverse, distal process absent or nearly so, basal elevation extending across basal area, not notched, as in *Corynura* (Fig. 142).

METASOMA. (38) Metasoma elongate but not petiolate. (39) Tergum VII abruptly convex, gradulus absent. (40) Anal lip of proctiger without postanal filaments. (42-44) Sterna IV-VI normal, sternum VI not notched. (45) Sternum VII broadly produced posteriorly to truncate projection bearing short setae; apodemes slightly recurved. Sternum VIII produced posteriorly into narrow median lobe bearing strong setae; laterally joining VII on posterior edge of apices of apodemes. Spiculum broad (Figs. 274-276).

(46) Gonobase (Figs. 331-334) with broad ventral bridge, dorsal lobes slightly projecting over gonocoxites. (47) Ventral gonostylus a large clear thin apical lobe, without setae ventrally, few setae dorsally. Parapenial lobe and basal process of gonostylus absent. Dorsal gonostylus a simple ridge. (48) Penis valve (Fig. 334) without ventral keel, without dorsal crest; lateral edge raised. *Dorsal bridge inserted on penis valves near apices.* (49) *Volsella* (Fig. 333) *greatly enlarged,* with transverse ridge opposite notch and longitudinal ridge above notch, inner apical angle produced ventrally.

Species of *Halictillus* are small (about 5-6 mm) dull metallic bluish-green weakly punctured bees extremely similar in general appearance to species of the widespread non-augochlorine subgenus *Dialictus* (of *Lasioglossum*), with which they are sympatric. The females of *Halictillus* can be separated from *Dialictus* principally by the strong outer veins of the forewing of *Halictillus;* the eyes are also more deeply emarginate. Males of *Halictillus* have long *Corynura*-like antennae and lack the pygidial plate of males of *Dialictus.* The mouthparts and male hidden sternal and genitalic structure of *Halictillus* indicate a close relationship with *Corynura.* Most species of *Corynura* are much larger and quite different in general appearance; those few *Corynura* with which *Halictillus* could possibly be confused can be distinguished by the pectinate tibial spur, basally roughened propodeum, and more strongly angulate epistomal sulcus of *Halictillus.* The metasoma of the male is not petiolate. *Rhectomia* is another genus of small dull metallic *Dialictus*-like augochlorine bees with which *Halictillus* could possibly be confused; see the discussion of that genus. *Halictillus* has seldom been separated from *Dialictus* in collections, so its geographic range is not easily ascertainable. I have seen specimens from southern Brazil and Argentina. About three species are known; there are probably less than ten species in all.

Genus **Rhinocorynura** Schrottky

Corynura (Corynuropsis) Cockerell, 1901, Proc. Acad. Natur. Sci. Philadelphia 53:220. (Type species: *Corynura (Corynuropsis) daruini* Cockerell, 1901, original designation.) Preoccupied. NEW SYNONYMY.

Rhinocorynura Schrottky, 1909, Rev. Mus. La Plata 16:147. (Type species: *Halictus (Corynura* vel *Corynuropsis) inflaticeps* Ducke, 1907, monobasic and original designation.)

Ctenocorynura Schrottky, 1914, Deut. Entomol. Z. 1914:628. (Type species: *Ctenocorynura vernoniae* Schrottky, 1914, monobasic and original designation.)

Corynuroides Sandhouse, 1943, Proc. U. S. Nat. Mus. 92:540. New name for *Corynuropsis* Cockerell. NEW SYNONYMY.

Female

HEAD (Figs. 114-116). (1) Epistomal sulcus forming obtuse angle. (2) *Clypeus usually flat, apical portion abruptly beveled, posterior marginal area scarcely indented, median or lateral spines or tubercles usually present.* (4) Preoccipital ridge usually rounded, carinate in *R. briseis. Vertex swollen above ocelli.* (5,6) Hypostomal floor about as long as wide, l/w = 1.06,

c/l = .20 (1 sp.). (7) Posterior flange of hypostoma projects beyond occiput. (8) Inner orbit of compound eye weakly to moderately emarginate, w/l = .099 to .129 (4 spp.). (11) *Labrum* (Figs. 143-144) *with distal process expanded, narrowed apically, fimbria on surface of process, keel low. Basal area short, basal elevation strongly notched or bituberculate.* (12) Mandible normal in small species, broad with subapical tooth produced (Fig. 165) in large species. (13) Distal portion of maxilla with base of galea distal to base of stipes, intermediate in position between that of *Augochlora* and *Corynura. Well-formed galeal comb present,* as in *Corynura* (Fig. 178). Inner strip with broad scale-like cuticular markings, long setae only at apex. (14) Maxillary palpus p/M = .29 to .41 (4 spp.). (15) Prementum with anterior conjunctival thickenings distal to its base, as in *Corynura* (Fig. 169) but prementum longer and more slender; pl/W = .55 to .59, pw/pl = .20 to .23 (4 spp.). (16) Salivary plate normal, broad V-shaped brace. (17) Glossa short, as in *Corynura,* gl/pl = .26 to .36, gl/W = .14 to .20 (4 spp.).

MESOSOMA. (19) *Pronotal dorsal ridge* (Fig. 186) *lamellate, forming flange from lateral angle to lobe.* Lateral angle may be produced beyond dorsal ridge, rounded or sharply angled. Lateral ridge sharply angled or rounded. (20) *Mesoscutum strongly produced over pronotum, lip high and sharp, usually slightly upturned and carinate.* (22) *Basal area of propodeum smooth, usually shiny, depressed transversely.* (24, 25) Marginal cell of forewing acute, cell long, mc/wl = .61 to .75 (4 spp.). (26) Small tibial spine present. (27) Hind tibial spur pectinate, teeth usually broad and rounded (Fig. 210). (29) Basitibial plate well-defined on all edges, narrowly rounded. (30) Anterior basitarsal brush weakly defined.

Male

HEAD. (35) Antenna not very long, reaching to scutellum or to just beyond propodeum, no plate areas; scape much longer than flagellomere, 2, sc/2 = 2.44 to 7.41, 2/1 = .94 to 1.15, 3/1 = 1.21 to 1.54, 10/1 = 1.18 to 1.72 (4 spp.). (36) Labrum with short triangular distal process, shorter than transverse basal area, basal elevation extending across basal area (based on 1 sp.).

METASOMA. (38) Metasoma usually elongate, not petiolate, rather compact and oval in 1 species. (39) Tergum VII abruptly convex apically, posterior margin emarginate medially, no gradulus. (40) *Anal lip of proctiger fringed with row of thin dark microtrichia,* proctiger frequently with cuticular striations and appearing stiffly extended (Fig. 234). (42-44) Sterna IV-VI normal, gradulus notched medially, posterior margin of VI weakly notched. (45) Sternum VII broadly produced posteriorly, truncate or emarginate, lined with setae. Apodemes slightly recurved. Posterior margin of sternum VIII not produced, or produced into median rounded lobe, without setae. Sternum VIII joins VII laterally at apices of apodemes. Spiculum narrow (Figs. 277-281).

(46) Gonobase (Figs. 337-344) with broad ventral bridge, rarely narrow, dorsal lobes weakly produced. (47) Ventral gonostylus variously produced apically (Figs. 337, 339, 341), lined with modified setae. Basal process of gonostylus present, bearing setae, small parapenial lobe present or absent. Dorsal gonostylus a narrow membranous swelling projecting from inner edge of lateral ridge, dorsally with small flap bearing long setae (Fig. 342) or with single long seta (Fig. 338). (48) Penis valve (Figs. 340, 343) with ventral keel, rounded dorsal crest bordering lateral longitudinal groove or depression, expanded laterally and medially. (49) Volsella (Fig. 344) more or less indented medially, apical inner angle more or less produced ventrally; base truncate or rounded.

The genus *Rhinocorynura* brings together a small but diverse group of species whose females are characterized by an enlarged head, broader than the thorax, with the vertex and genae produced, and an armed clypeus; both sexes have the mesoscutum and pronotum produced as described and the basal area of the propodeum smooth and usually shiny. Most species are rather variable in size, with the females highly variable in head size and clypeal armature. There appear to be three species groups, linked by intermediate species.

Species previously placed in *Corynuroides* are medium-sized, dark, metallic bees with the clypeal armature limited to coarse punctures or a median tubercle (Fig. 114), and the mandibles of the female are normal. The type species of *Corynuroides, Rhinocorynura briseis* (Smith), new combination (=*Corynura (Corynuropsis) darwini* Cockerell, according to Moure, 1944b), is largely dark with the mesoscutum and metasomal terga I and II coarsely punctate, and has a carinate preoccipital ridge; the genitalia are illustrated in Figs. 341-344. *Rhinocorynura crotonis* (Ducke), new combination, is dark metallic green and not coarsely punctate, and the preoccipital ridge is rounded. The genitalia more closely resemble those of the third species group mentioned below. *Corynuroides* might be deserving of subgeneric status if it were not for *crotonis* and the intermediate species discussed in the third group.

Rhinocorynura inflaticeps (Ducke), type species of the genus, is very variable in head size and clypeal armature of the female. Smaller specimens bear only a small central spine, and fit the description of the genus given by Schrottky (1909). Larger macrocephalic females (Fig. 115) have huge clypeal spines and fit the description by Schrottky (1914) of *Ctenocorynura*, as pointed out by Sakagami and Moure (1965). The male genitalia (Figs. 339-340) are somewhat different from those of species previously placed in *Corynuroides*. The bee is mostly dark, with dark anterior margins of the forewings.

The third group in *Rhinocorynura* has been recognized by a manuscript generic name by Moure; one of the species in it is rather large (about 9 mm), green, with a non-carinate mesoscutal lip and with the clypeus armed as shown in Fig. 116. The species rather resembles *R. inflaticeps* in the male genitalia (Figs. 337-338), hidden sterna (Fig. 281), and mandibles of the female (Fig. 165). However, a second small species belonging to this group on the basis of genitalic and mesoscutal characters is otherwise very similar to *R. crotonis* of the *Corynuroides* group; it is of the same size and coloring with unmodified female mandibles and a nearly unadorned clypeus.

Specimens of *Rhinocorynura* have been seen from Brazil, Bolivia, and Peru.

Cockerell (1901) first described a genus, *Corynuropsis,* to include species in this group, but, as pointed out by Sandhouse (1943), the name was preoccupied. The replacement name *Corynuroides* that Sandhouse (1943) proposed is subsequent to other names for this group and thus is a junior subjective synonym. Moure (1944b) discussed the validity and relationship of *Corynuroides,* considering it separate but closely related to *Rhinocorynura.* He did not know the male of *Rhinocorynura.*

Schrottky (1909a) proposed *Rhinocorynura* for a species previously placed conditionally in *Corynuropsis* Cockerell by Ducke (1907), based on the median spine of the clypeus of the female. Later, Schrottky (1914) proposed *Ctenocorynura* for a macrocephalic large-spined female which Moure (Sakagami and Moure, 1965) showed to be in the species *Rhinocorynura inflaticeps.* Sakagami and Moure (1965) discussed the head allometry of *R. inflaticeps* and synonymized *Ctenocorynura* with *Rhinocorynura.*

Genus **Corynurella,** new genus

(Type species: *Corynurella mourei,* new species.)

Female

HEAD (Fig. 117). (1) *Epistomal sulcus forming slightly acute angle.* (4) Vertex slightly swollen above ocelli. Preoccipital ridge rounded. (5, 6) Hypostomal floor over 1.5 times longer than wide, l/w = 1.83, c/l = .17 (1 sp.). (7) Posterior flange projects beyond occiput. (8) Inner orbit of compound eye rather weakly emarginate, w/l = .090 to .095 (2 spp.). (11) Labrum with distal process medially narrowly triangular, but projecting laterally from beneath posterior margin of basal area as rounded lobes, thus resembling *Rhinocorynura briseis* (Fig. 143); *basal elevation orbicular, strongly protuberant with apical surface flattened, similar to that of Pseudaugochloropsis* (Fig. 7). (13) Distal portion of maxilla with base of galea distal to base of stipes, as in *Rhinocorynura. Well-developed galeal comb present.* Inner strip with broad scale-like cuticular markings, long setae only at apex. (14) Maxillary palpus p/m = .44 to .45 (2 spp.). (15) Prementum with anterior con-

junctival thickenings distal to its base, as in *Rhinocorynura*, but longer and more slender, pl/W = .76 to .87, pw/pl = .17 to .19 (2 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa moderately long, much longer than in *Rhinocorynura*, about half length of prementum, gl/pl = .57, gl/W = .50 (1 sp.)*.

MESOSOMA. (19) *Pronotal lateral angle strongly carinate both anteriorly and laterally, angle produced as shown in Fig. 184**. Dorsal ridge sharply angled but not carinate behind lateral angle, *lateral ridge carinate*. (20) Mesoscutum slightly produced over pronotum, low and sharply angled. (22) *Basal area of propodeum longer than scutellum, shiny with fine, close, principally transverse striae**. (24, 25) *Marginal cell of forewing acute, extending almost to tip of wing*, mc/wl = .79 (1 sp.). *Stigma very large*. (27) Hind tibial spur pectinate, teeth rounded. (29) Basitibial plate defined on all edges, narrowly rounded. (30) Anterior basitarsal brush apparently absent.

Male

HEAD. (35) Antenna moderately long, reaching scutellum, no plate areas, sc/2 = 4.00, 2/1 = .96, 3/1 = 1.49, 10/1 = 1.77 (1 sp.). (36) Basal elevation of labrum extending across basal area, not notched; distal process not examined.

METASOMA. (38) Metasoma elongate but not petiolate. (39) Tergum VII abruptly convex apically, posterior margin not emarginate, no gradulus. (40) Anal lip of proctiger fringed with row of thin dark microtrichae, proctiger with cuticular striations and appearing stiffly extended, as in *Rhinocorynura* (Fig. 234). (42-44) Sterna IV to VI normal, gradulus bowed posteriorly and interrupted medially on sternum VI, posterior margin of VI weakly notched. (Sterna IV and V not dissected). (45) Sternum VII produced posteriorly, emarginate and lined with setae, apodemes slightly recurved. Posterior margin of sternum VIII not produced; sternum VIII joins VII laterally at apices of apodemes. Spiculum narrow (Fig. 282).

(46) Gonobase (Figs. 335-336) with broad ventral bridge, dorsal lobes rather strongly produced. (47) Ventral gonostylus an elongate, apically and medially projecting lobe, bearing a few setae at its apex. Basal process of gonostylus small, with setae, parapenial lobe absent. Dorsal gonostylus a long flap projecting from lateral ridge, bearing long setae at its apex. (48) Penis valve without ventral prong, dorsal surface with a wide, rounded, longitudinal ridge, abruptly bordered laterally by a longitudinal groove; valve expanded medially and laterally. (49) Volsella indented medially, apical inner angle produced; base truncate.

*Exceptions

I have placed a small unique female from Paraguay tentatively in this genus. It is greener with less abundant testaceous areas than the type species,

and the basal area of the propodeum is about as long as the scutellum, shiny and depressed transversely as in *Rhinocorynura* with striae almost absent. The lateral angle of the pronotum is produced similar to that of *Rhectomia* (Fig. 185). The glossa is shorter than that of *Corynurella mourei,* gl/pl = .38, gl/W = .29. The head is comparatively shorter and broader.

At present *Corynurella* contains with certainty only the new species *mourei,* described in Appendix 1. It is a medium-sized (about 7 mm), rather shiny, weakly punctate species, largely testaceous with the head and dorsum of the mesosoma with dark bluish-green tints and the tip of the metasoma dark. *Corynurella* is closely related to *Rhinocorynura;* this relationship is especially evident in the male hidden sterna and terga and the genitalia. The species can be easily separated from species of *Rhinocorynura* by the normal, rather shiny, and weakly punctured clypeus of the female and the different pronotal, mesoscutal, and propodeal structures. The exceptional species noted above indicates an even closer similarity of *Corynurella* with *Rhectomia.* Until the males of this species and of *Rhectomia* are known, the extent of this similarity cannot be determined. If the males are quite similar, *Corynurella* should perhaps be considered a subgenus of *Rhectomia. Corynurella mourei* is noteworthy for the enlarged stigma and long marginal cell, obvious at a glance. Specimens of *Corynurella* have been seen from southern Brazil and Peru.

Derivation of *Corynurella:* Diminutive of *Corynura* (feminine).

Genus **Rhectomia** Moure

Rhectomia Moure, 1947, Publ. avulsas Mus. paranaense no. 3:9. (Type species: *Rhectomia pumilla* Moure, 1947, monobasic and original designation.)

Female

HEAD (Fig. 118). (1) Epistomal sulcus forming obtuse angle. (4) Vertex swollen above ocelli. Preoccipital ridge rounded. (5, 6) Hypostomal floor longer than wide. (8) Inner orbit of compound eye rather weakly emarginate, w/l = .109 (1 sp.). (11) *Labrum with distal process broadly triangular, as wide as basal area; basal elevation bituberculate.* (13) Distal portion of maxilla with base of galea distal to base of stipes, as in *Rhinocorynura. Well-developed galeal comb present.* Inner strip with broad scale-like cuticular markings, long setae only at apex. (14) Maxillary palpus p/M = .42 (1 sp.). (15) Prementum with anterior conjunctival thickenings distal to its base, as in *Rhinocorynura,* pl/W = .72, pw/pl = .19. (16) Salivary plate normal, V-shaped brace. (17) Glossa rather short, gl/pl = .27, gl/W = .20 (1 sp.).

MESOSOMA. (19) *Pronotal lateral angle strongly produced as in Fig. 185, carinate anteriorly and laterally, ending laterally above dorsal ridge.* Dorsal ridge sharply angled but not carinate. *Lateral ridge carinate.* (20) Mesoscutal

lip low but produced over pronotum, abruptly rounded, not narrowed. (22) *Basal area of propodeum long, smooth, without striae.* (24, 25) Marginal cell of forewing acute, not greatly lengthened, mc wl = .60 (1 sp.); stigma not enlarged. (26) Weakly defined hind tibial spine present. (27) Hind tibial spur pectinate, teeth rounded. (29) Basitibial plate defined on all edges, narrowly rounded. (34) Anterior basitarsal brush apparently absent.

Rhectomia is known only from the type species, *R. pumilla* Moure, a small (about 5 mm) dull metallic green bee closely resembling in general appearance species of *Dialictus* but lacking the weakened outer wing veins in the female. The pronotal structure (Fig. 185) separates *Rhectomia* from other genera except the quite similar *Corynurella*. The differences in the marginal cell, stigma, and labrum aid in separating these two genera; they appear to be closely related (see discussion under *Corynurella*), but further decisions concerning their status cannot be made until the male of *Rhectomia* is known. *Rhectomia* is known only from southern Brazil.

Moure (1947) described in detail the type species and gave the characteristics of the genus.

Genus **Neocorynura** Schrottky

Female

HEAD (Fig. 119). (1) Epistomal sulcus forming obtuse angle. (4) *Preoccipital ridge carinate or lamellate.* (5, 6) Hypostomal floor less than 1.5 times as long as wide, l/w = .95 to 1.30 (4 spp.), c/l = .26 to .37 (5 spp.). (8) Inner orbit of compound eye deeply emarginate, w/l = .135 to .182 (8 spp.). (12) Mandible usually normal, occasionally with tip expanded, some species with subapical tooth produced so mandible appears bidentate at apex, rarely supplementary tooth present so mandible tridentate. (13) Distal portion of maxilla normal, inner strip with scale-like cuticular markings and setae only on outer border near apex. Small poorly formed galeal comb sometimes present, usually of 6 or less teeth. (14) Maxillary palpus, p/M = .35 to .52 (17 spp.). (15) Prementum normal, pl/W = .57 to .82, pw/pl = .17 to .25 (17 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa usually 0.3 to 0.5 length of prementum, gl/pl = .34 to .59, gl/W = .22 to .48 (13 spp.).

MESOSOMA. (19) Pronotal lateral angle usually strongly produced (Fig. 187), sometimes weakly so or rounded; lateral ridge carinate or lamellate; dorsal ridge carinate. (20) *Mesoscutum usually narrowed anteriorly, mesoscutal lip usually narrow, high, projecting forward and sharply angled,* occasionally not narrowed, normal. (22) Basal area of propodeum usually striate, occasionally completely smooth or with weak basal striae. (23) *Propodeum usually narrowed posteriorly, lateral carinae little diverging,* rarely not narrowed. (24, 25) Marginal cell of forewing acute or very narrowly truncate

and appendiculate, mc/wl = .55 to .61 (7 spp.). (27) *Hind tibial spur pectinate* (Fig. 211). (29) Basitibial plate well defined on all edges, narrowly rounded. (30) Anterior basitarsal brush weakly defined.

METASOMA. (31-34) Sterna and terga usually normal, rarely pseudopygidial area of sternum V with scale-like setae bordering median slit.

Male

HEAD. (35) Antenna usually long, frequently surpassing propodeum, sc/2 = 1.43 to 2.40, 2/1 = 1.28 to 2.94, 3/1 = 1.60 to 2.94, 10/1 = 1.97 to 3.68 (11 spp.). (36) Labrum (Fig. 146) transverse, distal process very slightly developed, basal elevation extending across basal area.

METASOMA. (38) *Metasoma narrow, usually petiolate* (Fig. 222) *with first tergum decidedly narrower than the following,* occasionally first segment not decidedly narrowed. Sterna I and II long and narrow (Fig. 237). (39) Tergum VII abruptly convex apically, gradulus usually not or weakly defined, rarely well defined. (40) Anal lip of proctiger without post-anal filaments. (42-44) Sterna IV to VI normal, apex of VI weakly notched or entire. (45) Sternum VII usually not or slightly projecting posteriorly, rarely strongly projected into a median, rounded or truncate process, posterior margin or process with setae. Median posterior process of sternum VIII produced into long rounded process, usually surpassing posterior margin of sternum VII and without or with few setae, rarely with many setae; sternum VIII joining VII near apices of apodemes. Spiculum narrow (Figs. 283-285).

(46) Gonobase (Figs. 345-351) with narrow ventral bridge, dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus variable, see subgeneric descriptions. Dorsal gonostylus a simple ridge, usually flanged, occasionally with membranous process or inner border of flange or rarely with medially directed flap. (48) *Penis valve narrow, very long, surpassing gonostyli, without crest, inner edge higher, tip usually prolonged and curved* (Fig. 348). (49) Volsella large, more or less quadrate, inner apical margin usually more or less indented (Fig. 347).

Neocorynura is possibly the largest augochlorine genus, with species recorded from Mexico to Argentina. Typical species are medium-sized and largely black with some bright green reflections, although many species are bright green similar to typical *Augochlora*. The end of the mesosoma is narrowed in typical species and the metasoma narrowed basally and petiolate in the male, giving the bees a striking resemblance to polybiine wasps, heightened by darkly pigmented anterior margins of the forewings in some species. This general appearance is seldom duplicated by other augochlorine genera throughout *Neocorynura's* range except where it overlaps *Corynura* in the South Temperate Zone.

However, enough exceptions occur to make some species difficult to recognize as *Neocorynura* without examination of genitalia. At present I recognize

only one subgenus besides *Neocorynura s. s.;* other groups are too poorly represented and defined to merit separate status. Association of the sexes is particularly a problem.

Subgenus **Neocorynura** Schrottky

Cacosoma Smith, 1879. Descriptions of new species of Hymenoptera in the collection of the British Museum:39. Preoccupied. (Type species: *Cacosoma discolor* Smith, 1879, designated by Sandhouse, 1943.)

Neocorynura Schrottky, 1910. Deut. Entomol Z. 1910:540. New name for *Cacosoma* Smith, preoccupied.

Female

(11) Labrum (Fig. 145) with distal process narrow, usually shorter than or subequal to basal area, distal keel with edge rounded or slightly flattened. Basal elevation longitudinal, raised above basal area, gradually rounded or sharply angled. (4) Preoccipital ridge carinate, not exceptionally flanged. (19) Lateral ridge of pronotum carinate, not strongly lamellate. (31) Pseudopygidial area of metasomal sternum V with normal setae or scale-like setae.

Male

(35) Antenna usually long, plate areas frequently present. (47) Ventral gonostylus of genitalia (Fig. 345) a medially directed long flap, bearing setae in various patterns on flattened ventral surface with anterior ("lower") edge frequently prolonged and usually thin. Basal process of gonostylus present as small lobe without setae. Dorsal gonostylus (Fig. 346) without inner extension or with small membranous lobe. (48) Penis valve (Fig. 348) without ventral prong and with apex variously prolonged, curved, or otherwise modified.

At present *Neocorynura s. s.* contains all species of *Neocorynura s. l.* but one. Typical species have a narrowed propodeum, petiolate metasoma in the male, rounded basal elevation on the female clypeus, normal female mandible, and normal pseudopygidial area on tergum V.

A number of species from the Andes do not have tergum I of the male metasoma abruptly narrower than II, and do not have a strongly narrowed mesoscutum anteriorly nor produced pronotal lateral angles. Most species of this group have a granular propodeum with weak striae and do not obviously resemble *Neocorynura,* although most other characters are similar. The scutellum of one male is strongly bituberculate, similar to that of *Chlerogas.*

A second group of five females is characterized by strongly bidentate or tridentate mandibles and scales lining the pseudopygidial area. The basal elevation of the clypeus is strongly angled at the division of the upper and lower surfaces. Most, but not all, specimens do not have the propodeum narrowed. The one male associated with a female (*Neocorynura rufa* Michener) of this group has the posterior process of metasomal sternum VIII

greatly elongate, much surpassing the straight margin of sternum VII, with setae at its apex, and the inner edge of the penis valve produced and strongly elevated. A second male, not associated with any female, shares these characteristics. If this correlation of characters holds true when the sexes of more species are associated, the group deserves subgeneric status. In general appearance, bees of this group resemble typical *Neocorynura*.

Smith's original *Cacosoma* included species of both *Corynura* and the present *Neocorynura*. Schrottky (1910), in proposing *Neocorynura* to replace *Cacosoma*, stated that it was in no way synonymous with *Corynura*. However, he did not adequately separate the two genera, and most workers prior to 1940 (e.g., Herbst, 1917) except Schrottky and Cockerell (1919b) placed species now placed in *Neocorynura* in *Corynura* or *Rhopalictus*. Alfken (1926) correctly separated *Corynura* from species now placed in *Neocorynura*, except for *Corynura chilensis* (Spinola), thus he used the name *Rhopalictus* for *Neocorynura*.

Well known species of *Neocorynura s. s.* include *N. pubescens* (Friese) from Central America, and *N. pilosa* (Smith) and *N. jucunda* (Smith) from South America.

Subgenus **Neocorynuroides,** new subgenus

(Type Species: *Halictus rhytis* Vachal, 1904a.)

Female

(11) Labrum with distal process longer than basal area, distal keel flat-topped at apex. Basal elevation transverse, very low. (12) Mandible with apex slightly expanded and subapical tooth rather large, but apex not bidentate. (4) Preoccipital ridge strongly lamellate, flange recurving over genae. (19) Lateral ridge of pronotum strongly lamellate. (31) Pseudopygidial area of metasomal sternum V with scale-like setae bordering median slit.

Male

(35) Antenna not as long as in *Neocorynura s. s.*, reaching propodeum, no plate areas. (47) Ventral gonostylus of genitalia with seta-bearing surface facing inward (Figs. 349-350). No basal process. Dorsal gonostylus a thin clear flap (Fig. 351). (48) Penis valve with ventral prong, tip of valve not prolonged or modified.

Neocorynuroides contains only one known species, *Neocorynura rhytis* (Vachal). It is a distinctive small species, about 5.5 mm long, with the female mesoscutum black with purple tints and cut by transverse striae radiating from the median line, these striae occasionally light or absent. The male mesoscutum is green and lacks the striae. *N. rhytis* has a relatively short and wide proboscidial fossa, hypostomal l/w = .95 and c/l = .264; the mouthparts are correspondingly short and wide, pl/W = .57 to .58 and pw/pl =

.24 to .25 for 2 specimens. The maxillary palpus is not long, all segments being short and conical. The mesoscutum is strongly narrowed and its lip is elevated and produced forward at a sharp angle; the lateral angles of the pronotum are also strongly produced. The propodeum is narrowed posteriorly and its basal area bears strong striae. The male metasoma is petiolate.

The naming of a new subgenus is justified largely on the basis of the distinctive male genitalia, the gonostyli in particular being quite different from those of any *Neocorynura s. s.* I have seen specimens of *N. rhytis* (Vachal) from Bolivia and Peru.

Derivation of *Neocorynuroides:* Like *Neocorynura* (masculine).

Genus **Paroxystoglossa** Moure

Paroxystoglossa Moure, 1941, Arq. Zool. Estado São Paulo 2:59. (Type species: *Oxystoglossa jocasta* Schrottky, 1911, original designation.)

Female

HEAD (Fig. 120). (1) Epistomal sulcus forming obtuse angle. (4) Preoccipital ridge sharply angled*. (5, 6) Hypostomal floor about as long as wide, l/w = .96 to 1.20, c/l = .05 to .24 (3 spp.). (8) Inner orbit of compound eye moderately emarginate, w/l = .083 to .115 (3 spp.). (11) Labrum (Fig. 147) with distal process triangular, narrower than basal area; basal elevation suborbicular, protuberant, with distal surface somewhat flattened and indented or notched medially. (13) Distal portion of maxilla normal, inner strip with rather narrow scale-like cuticular markings, long setae only at apex. (14) Maxillary palpus, p/M = .27 to .40 (4 spp.). (15) Prementum normal, pl/W = .61 to .81, pw/pl = .16 to .21 (4 spp.). (16) Salivary plate normal. (17) Glossa of moderate length, less than half length of prementum, gl/pl = .35 to .45, gl/W = .22 to .36 (4 spp.).

MESOSOMA. (19) Pronotal lateral angle rounded, either produced (Fig. 188) or not. Lateral ridge sharply angled or rounded, dorsal ridge carinate. (20) *Mesoscutum narrowed anteriorly, lip high, projecting forward and sharply angled;* when lateral angle not produced, mesoscutum not narrowed and lip rounded, not high. (22) Basal area of propodeum with weak plicae or roughening basally, smooth apically. (23) *Propodeum not narrowed posteriorly.* (24, 25) Marginal cell of forewing narrowly truncate and appendiculate, or acute, mc/wl = .58 to .66 (3 spp.). (27) *Hind tibial spur serrate,* as in *Corynura chilensis* (Fig. 206). (29) Basitibial plate well defined on all edges, narrowly rounded. (30) Anterior basitarsal brush poorly defined or absent.

Male

HEAD. (35) *Antenna long, reaching to or beyond propodeum, scape short; flagellomere 2 about twice length of 1, longer than or subequal to length of 10,** sc/2 = 1.29 to 2.17, 2/1 = 1.99 to 2.13, 3/1 = 2.10 to 2.24, 10/1 = 1.78

to 2.17 (3 spp.). *No plate areas.* (36) Labrum transverse, distal process little developed, basal elevation extending across basal area, as in *Neocorynura* (Fig. 146).

METASOMA. (38) Metasoma rather broad to narrow and elongate, but not petiolate, segments I and II not decidedly long and narrow. (39) Tergum VII gradually convex apically, gradulus absent or weakly defined. (40) Anal lip of proctiger without post-anal filaments. (42) *Sternum IV* (Fig. 238) *with shiny, median apical depression bordered by sharply raised ridges, or posterior margin emarginate, central postgradular area depressed and shiny.* (43) *Sternum V* (Fig. 239) *with median shiny depression usually bordered by strong ridges or elevations and modified setae.* (44) Sternum VI (Fig. 240) deeply notched, strongly depressed apically. (45) Sternum VII produced posteriorly into rounded or subtruncate seta-bearing median process, frequently with median ridge; apodemes recurved slightly anteriorly. Sternum VIII produced posteriorly into small median lobe, bearing few long setae or without setae; laterally joining VII near apices of apodemes. Spiculum rather narrow (Fig. 286-288). (46) Gonobase (Figs. 352-355) with narrow ventral bridge, dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus an elongate lobe bearing long setae on its dorsal and outer portion of ventral surfaces. Basal process of gonostylus and parapenial lobe absent. Dorsal gonostylus a medially directed thin narrow flap. (48) Penis valve (Fig. 355) with ventral prong and rounded dorsal crest posterior to dorsal depression; valve somewhat expanded laterally and medially, with small projection on lateral margin near apex of crest. (49) Volsella (Fig. 354) with inner edge emarginate, inner apical angle somewhat prolonged, base truncate.

*EXCEPTIONS

The preoccipital ridge of many, but not all, males is carinate. The antennae of the males of two species are much shorter than described above, with the scape longer and flagellomere 2 not much longer than 1; $sc/2 = 3.80$, $2/1 = 1.00$, $3/1 = 1.11$, $10/1 = 1.52$ (1 sp.).

Paroxystoglossa is a diverse genus of about 9 species of medium sized, variously colored bees. The females of most species are largely dark-colored with a narrowed mesoscutum and produced pronotal lateral angles and strongly resemble many *Neocorynura*. The tibial spur is the best characterisitc to separate female *Paroxystoglossa* from *Neocorynura;* the non-carinate preoccipital ridge and unnarrowed propodeum are also aids. A few species of *Paroxystoglossa* are usually bright green in the female, without a decidedly narrowed mesoscutum or produced lateral angles. They are rather nondescript green bees best recognized by their tibial spurs.

Males are usually green, rarely dark, and typically have long antennae and an elongate metasoma. Metasomal sterna IV and V are characteristically

modified and serve to separate externally these bees from species of *Neocorynura;* these modifications range from strong ridges on both sterna to more gradual shiny depressions with the fourth sternum emarginate. The genitalia of *Paroxystoglossa* are quite different from those of *Neocorynura*. The femora of some males are swollen and the males ventrally on the head, mesosoma, and legs usually bear long plumose hairs. The bright green males of two species are quite different in general appearance, being compact with short antennae and non-carinate preoccipital ridges; the metasomal sterna of these species are strongly modified. Species of *Paroxystoglossa* are known from southern Brazil to Argentina.

Moure (1941a) described *Paroxystoglossa* for two Brazilian species Schrottky had placed in *Oxystoglossa*. Moure (1960a) has recently published a specific revision to *Paroxystoglossa,* including a key to the 9 species that he has recognized.

Genus **Andinaugochlora,** new genus

(Type species: *Andinaugochlora micheneri,* new species.)

Female

HEAD (Fig. 121). (1) *Epistomal sulcus forming right or slightly acute angle.* (4) Preoccipital ridge sharply angled or carinate. (5, 6) Hypostomal floor longer than wide, l/w = 1.49, c/l = .43 (1 sp.). (7) Posterior flange projects beyond occiput. (8) Inner orbit of compound eye deeply emarginate, w/l = .169 to .176 (2 spp.). (11) Labrum (Fig. 148) with distal process narrow and triangular, shorter than basal area. Basal elevation ovate, rounded, strongly protuberant. (13) Distal portion of maxilla with or without small galeal comb, as in *Neocorynura;* inner strip with narrow scale-like cuticular markings, long setae only at apex. (14) Maxillary palpus, p/M = .28 to .33 (2 spp.). (15) Prementum normal, pl/W = .70 to .73, pw/pl = .16 to .18 (2 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa moderately long, gl/pl = .41 to .52, gl/W = .30 to .36 (2 spp.).

MESOSOMA. (19) *Pronotal lateral angle not produced, forming obtuse angle.* Dorsal ridge weakly carinate; lateral ridge abruptly rounded. (20) Mesoscutum not narrowed anteriorly, lip rounded. (22) Basal area of propodeum granular, weakly plicate basally. (23) Posterior surface not exceptionally narrowed, unlike *Neocorynura.* (24, 25) Marginal cell of forewing narrowly truncate and appendiculate, mc/wl = .59 (1 sp.). (27) *Hind tibial spur pectinate* (Fig. 212). (29) *Basitibial plate well defined posteriorly, obsolescent anteriorly, sharply rounded* (Fig. 203). (30) Anterior basitarsal brush well defined.

Male

HEAD. (35) *Antenna very long, reaching beyond propodeum, scape short, flagellomere 2 over 1.5 times length 1, plate area present,* sc 2 = 1.63 to 2.03,

2/1 = 1.59 to 2.16, 3/1 = 1.89 to 2.16, 10/1 = 2.45 to 2.94 (3 spp.). (36) Labrum transverse, distal process little developed, basal elevation extending across basal area, weakly notched or entire, as in *Neocorynura* (Fig. 146).

METASOMA. (38) Metasoma elongate but not petiolate, segments I and II not very long and narrow. (39) Tergum VII more or less abruptly convex apically, gradulus weakly defined or absent. (40) Anal lip of proctiger without post-anal filaments. (42, 43) Sterna IV and V not modified, postgradular area of V centrally somewhat depressed, with short setae, laterally with longer setae. (44) *Apex of sternum VI* (Fig. 241) *strongly notched, with deep concavities to either side of notch and apical margin curved ventrally*, median ridge between concavities with modified setae. (45) Posterior margins of sterna VII and VIII produced medially, VII and occasionally VIII bearing setae. Apodemes of VII little recurved, sternum VIII joining VII at apices of apodemes. Spiculum broad (Figs. 290-292).

(46) Gonobase (Figs. 358-361) with narrow ventral bridge, dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus a medially directed lobe bearing modified setae on outer (ventral) edge, prolonged caudally above gonocoxite*. Basal process of gonostylus and parapenial lobe absent. Dorsal gonostylus a narrow, thin, medially projecting flap, arising from inner edge of dorsal ridge*. (48) Penis valve (Fig. 360) with ventral prong and dorsal crest distal to dorsal depression; valve with high flange on medial edge of dorsal depression. (49) Volsella (Fig. 361) more or less rounded basally, with deep depression above notch*.

*EXCEPTIONS

In one species, the caudal prolongation of the ventral gonostylus of the male genitalia forms a prolonged thin flange, and the dorsal gonostylus is a broader flap, expanded and spiculate apically. In this species, the volsella is notched apically and ridged, but does not bear a deep depression.

Andinaugochlora is known from four species from the high Andes. (All specimens thus far have been collected at altitudes of over 2500 meters.) The bees are largely green, sometimes with cupreous, yellow, or blue tints. The known females have striate pleurae. In general the bees are long-haired and largely granular and closely resemble the high Andean complex of *Neocorynura* mentioned in the discussion of that genus. The females of *Andinaugochlora* can be distinguished from *Neocorynura* by the epistomal sulcus and basitibial plate. The males are most easily recognized externally by the sixth metasomal sternum; the genitalia are quite different from those of *Neocorynura*.

The type species is described as new in Appendix 1. The alpine South American halictines are very poorly represented in collections, so an accurate estimate of the number of species and range of morphological variation in

Andinaugochlora must await further field work. Specimens of *Andinaugochlora* have been seen from Colombia, Ecuador and Peru.

Derivation of *Andinaugochlora:* Andean, plus *Augochlora* (feminine).

Genus **Chlerogas** Vachal

Chlerogas Vachal, 1904. Misc. Entomol. (Narbonne) 12:127. (Type species: *Halictus chlerogas* Vachal, 1904a, monobasic.)

Male

HEAD (Figs. 136-137). (1) *Epistomal sulcus forming right angle.* (3) *Malar area greatly elongate, twice as long or longer than distance between mandibular articulations, head very elongate.* (4) Preoccipital ridge sharply angled, not carinate. (8) Inner orbit of compound eye moderately emarginate (in male). (35) Antenna long, reaching to propodeum or beyond, plate areas present, sc 2 = 2.37, 2 1 = 1.28, 3/1 = 1.61, 10/1 = 2.04 (1 sp.). (36) Labrum with basal elevation extending across basal area, weakly notched or entire; distal process not examined. (13-16) Mouthparts not dissected, not greatly narrowed or obviously modified, maxillary palpi rather long and slender.

MESOSOMA. (19) Pronotal lateral angle obtuse, not produced, rounded; lateral ridge rounded; dorsal ridge sharply angled but not carinate. (20) Mesoscutum not narrowed anteriorly, lip low and rounded. *Scutellum produced into two large tubercles.* (22) Basal area of propodeum with fine regular plicae or weak plicae basally, smooth posteriorly. (23) Posterior surface of propodeum strongly narrowed *(hirsutipennis)* or not *(C. chlerogas)*, lateral carinae slightly diverging. (24, 25) Marginal cell of forewing acute, mc wl = .62 (1 sp.). (37) *Inner hind tibial spur pectinate, with 3-5 long teeth.*

METASOMA. (38) Metasoma elongate, not petiolate. Tergum VI of *C. hirsutipennis* produced laterally into lamellae bordering shiny depressions, visible dorsally without dissection; not produced in *C. chlerogas.* (39) Tergum VII gradually convex, with distinct gradulus. (40) Anal lip of proctiger without post-anal filaments. (42) Sternum IV normal (not dissected). (43) Sternum V normal or emarginate, with long setae on postgradular area (not dissected). (44) Sternum VI (Fig. 242) deeply notched, medially depressed with longitudinal keel. (45) Sternum VII produced posteriorly into rounded lobe bearing short setae, apodemes little recurved. Sternum VIII similarly produced posteriorly, without setae; laterally joining VII at apices of apodemes. Spiculum moderately broad (Fig. 289).

(46) Gonobase (Figs. 356-357) very large, ventral bridge narrow, dorsal lobes moderately produced. Ventral bridge of gonocoxites expanded medially. (47) Ventral gonostylus an apically projecting lobe, with setae only on apical edge of flattened ventral surface, also on dorsal surface. Basal process of gonostylus and parapenial lobe absent. Dorsal gonostylus an expanded, clear,

thin lobe with cuticular wrinkles, projecting from seta-bearing rounded lateral ridge. Narrow thin projection extends apically from anterior margin of dorsal gonostylus, ventral or dorsal to rest of gonostylus. (48) Penis valve narrow, no ventral prong, rounded dorsal ridge posterior to small dorsal depression; narrow longitudinal depression lateral to dorsal ridge. (49) Volsella indented on inner margin, notch near apex, base truncate.

Chlerogas is known from two rather large (about 12 mm) weakly punctate species, one bright green and the other largely blackish. Through the courtesy of Dr. Richard Froeschner of the United States National Museum, I have been able to study the externally visible features of the holotype of *Chlerogas hirsutipennis* Cockerell. Dr. Henry Townes has graciously lent me a male specimen of *Chlerogas* which he collected at Machu Picchu, Peru, which agrees with the description that Vachal (1904a) gave for *C. chlerogas* (Vachal), and he allowed me to dissect its genitalia. The extraordinary development of the head and the bituberculate scutellum readily distinguish these species from species of any other genera. A male specimen of *Neocorynura* also shares the character of the bituberculate scutellum. The female is unknown, as discussed below, and there is no reason to surmise that the species of *Chlerogas* are social parasites, as suggested by Vachal (1904a) and Cockerell (1919a). Specimens have been recorded only from Peru.

Vachal (1904a) described his specimen of *Halictus chlerogas* as female, due to its pectinate tibial spur and tarsal claw. The end of the abdomen and the antennal flagella had apparently been lost ("Le funicle et le bout d'abdomen manquant. . . ."). He thus proposed a new genus for the species if it were to be proven to be a social parasite, and said that the name of the species should become *Chlerogas latitans* Vachal, a change which is not permitted by the International Code, as noted by Cockerell (1919a). Moure (personal communication) has examined the holotype of *Chlerogas chlerogas* in the Paris Museum and found it to be a male.

Cockerell (1919a) in describing the second species of *Chlerogas,* agreed with Vachal's suggestion about the social parasitic appearance of the bees and the validity of the separate genus. He described the holotype of his new species, *Chlerogas hirsutipennis,* as a female. However, the only known specimen is definitely a male.

Genus **Augochloropsis** Cockerell

Female

HEAD (Fig. 122). (1) Epistomal sulcus forming obtuse angle. (4) Preoccipital ridge sharply angled or carinate. (5, 6) Hypostomal floor longer than wide, l/w = 1.39 to 1.76, c/l = .56 to .75 (7 spp.). (7) Posterior flange projects beyond occiput. (8) Inner orbit of compound eye moderately emargi-

nate, w/l = .101 to .157 (13 spp.)*. (11) *Labrum* (Fig. 151) *with distal process expanded, as wide as basal area, distal keel projecting beyond apex, with lateral extensions near basal area. Basal elevation strongly notched medially. Labral fimbria on anterior surface of distal process.* (13) Distal portion of maxilla normal, apical lobe well-defined on outer surface, inner strip with broad scale-like cuticular markings and long setae only at apex. (14) Maxillary palpus, p/M = .28 to .38 (21 spp.). (15) Prementum normal, pl/W = .54 to .70, pw/pl = .12 to .20 (23 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa 1/3 to 1/2 length of prementum, gl/pl = .33 to .49, gl/W = .21 to .31 (21 spp.)*.

MESOSOMA. (19) *Pronotal dorsal ridge strongly lamellate, forming flange from lateral angle to lobe* (Fig. 189)*, lateral angle sometimes produced beyond flange. Lateral ridge rounded, rarely sharply angled. (20) Mesoscutum not narrowed anteriorly, lip usually broadly rounded. (21) *Tegula with inner posterior angle produced* (Fig. 199). (23) Posterior surface of propodeum wide ventrally, lateral carinae subparallel and arising considerably lateral to posterior submarginal pits. (24, 25) Marginal cell of forewing truncate, usually appendiculate, mc/wl = .44 to .55 (11 spp.). (27) *Hind tibial spur pectinate, all teeth long* (Fig. 213). (29) *Basitibial plate very short, extending barely past apex of femur, all edges defined* (Fig. 204). (30) Anterior basitarsal brush well defined.

METASOMA. (31, 32) Terga V and VI normal, pygidial plate may be notched apically. (34) Sternum IV with gradulus present basally, rarely obsolescent.

Male

HEAD. (35) Antenna not greatly elongate, sc/2 = 3.10 to 4.69, 2/1 = .81 to 1.30, 3/1 = .99 to 1.60, 10/1 = 1.12 to 1.75 (9 spp.). No plate areas. (36) *Labrum* (Fig. 152) *with distal process expanded as in female,* basal elevation notched medially and extending across basal area.

METASOMA. (39) Tergum VII (Fig. 226) gradually convex apically, gradulus present and nearing antecosta medially, a line extending from gradulus to spiracle*. (40) Anal lip of proctiger without or with short postanal filaments (Fig. 235). (42) *Sternum IV laterally produced into caudally directed processes, bearing setae, apical margin with median triangular lobe, gradulus meeting antecosta medially* (Figs. 243-244)*. (43) Sternum V unmodified or with hair tufts and marginal incisions (see subgeneric descriptions). (44) Sternum VI notched medially, truncate, post-gradular area laterally more or less elevated to form flanges surpassing dorso-lateral areas, setae densest medially (Figs. 246-247). (45) Sternum VII with truncate or rounded median posterior projection, bearing setae; apodemes slightly recurved anteriorly. Sternum VIII with posterior median projection variously developed,

usually bilobed, occasionally nearly absent, without setae or with few small setae; laterally joining sternum VII near apices of apodemes, spiculum broad (Figs. 293-297).

(46) Gonobase (Figs. 362-369) with narrow or membranous ventral bridge, dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus complex, apically a seta-bearing lobe; continued basally as a broad lobe bearing small setae on ventral surface and strong setae on apical edge, and with medial extension bearing a more or less well-defined long thin process. Basal process of gonostylus absent. Dorsal gonostylus a curved transparent lobe, usually bearing cuticular markings or dark patch of setae on inner surface. (48) Penis valve (Figs. 364, 369) with small ventral keel and pronounced darkly pigmented dorsal crest apical to dorsal depression; valve expanded medially and laterally. (49) Volsella (Fig. 368) with transverse ridge and depression below notch, apical median angle prolonged into ventrally (outwardly) directed projection.

*EXCEPTIONS

One species with an exceptionally broad head and produced genae has the eyes less emarginate, w/l = .083. Another species with an elongate head has the mouthparts also somewhat elongate, pl/W = .83 and gl/W = .38. A few species have the pronotal dorsal ridge less developed, strongly carinate but not forming a definite flange. One species lacks a gradulus on metasomal tergum VII of the male. Four males examined do not have distinct processes on sternum IV, although the apical margins are somewhat produced laterally (Fig. 245), and one species also lacks the median apical triangular lobe.

Augochloropsis is one of the largest of the augochlorine genera, represented from Canada to Argentina. Most of its members are medium sized to large, brilliant green or blue, frequently partly crimson or golden. The genus is easily recognized by a number of distinctive characters; the pronotum, tegulae, and labrum being the most easily observed without dissection. Metasomal sternum IV of the male is quite distinctive but the lateral processes are not usually visible without dissection, although when long they frequently protrude from beneath overlapping terga. In addition, many (but not all) species have a distinctive row of thick setae subapically on metasomal terga I to III (Fig. 224), called the "vibrissae," which led Vachal (1911) to name the group the *Halicti vibrissati*. As mentioned in the historical review, most of the species in *Augochloropsis* described prior to 1930 were placed in *Augochlora*.

Augochloropsis can be divided into two subgenera, well separated by male genitalic and sternal characters but poorly so in the female. These subgenera contain some small species groups which I do not at present consider worthy of subgeneric status.

Subgenus **Augochloropsis** Cockerell

Augochlora (Augochloropsis) Cockerell, 1897, Can. Entomol. 29:4. (Type species: *Augochlora subignita* Cockerell, 1897, original designation.)

Female

(22) Basal area of propodeum deeply and regularly pitted or strongly striate basally, smooth apically.

Male

(36) Distal process of labrum truncate or notched apically, with weak median groove on process. (39) Metasomal tergum VII with gradulus medially notched (Fig. 227). (42) Metasomal sternum IV with thick long setae anterior to lateral processes and on inner edges of processes, not on rounded apices (Fig. 243)*. (43) Sternum V with apical margin variously notched, postgradular area with long curved setae, frequently with median tuft of erect setae. (44) Sternum VI with wide apical postgradular flanges, variously modified (Fig. 246). (45) Sternum VII with narrow median posterior projection, sometimes ridged (Fig. 296)*. (47) *Ventral gonostylus apically bearing a row of strong, flattened, regular setae* (Figs. 362-363). (48) *Penis valve with very high crest* (Figs. 364-365).

*Exceptions

See exceptions of *Augochloropsis s. l.* In three species with the lateral projections of metasomal sternum IV not developed, rows of strong setae are present anterior to the apical margin in typical position. One species examined has the median posterior projection of sternum VII more broadly rounded than as shown in Fig. 296, and one other has the projection narrowly truncate, with few setae.

Cockerell (1897) first described *Augochloropsis* as a subgenus of *Augochlora* on the basis of the pectinate hind tibial spur, and later (1900) gave more differences between the two groups. Schrottky (1906) divided *Augochloropsis* into two subgenera, *Paraugochloropsis* (*Halicti vibrissati* of Vachal) with setal borders on the metasomal terga and *Pseudaugochloropsis* (*Halicti sericei*) without setal borders. In a later paper, Schrottky (1909b) reserved *Augochloropsis* for bees similar to *Augochlora,* but with a 3-toothed tibial spur, and named *Tetrachlora* as a subgenus of *Augochlora* for species with a 4-toothed spur, and retained *Augochlora (Paraugochloropsis)* for species with a 5-7-toothed spur and abdominal vibrissae. After learning of the identity of the type species of Cockerell's *Augochloropsis,* Schrottky (1910) proposed *Paraugochlora* for the group he previously considered as *Augochloropsis,* and referred *Augochloropsis* to the group he had called *Tetrachlora, Augochloropsis* being the senior synonym.

The first adequate description of *Augochloropsis* was given by Vachal (1911), who called the group the *Halicti vibrissati.* Prior to 1937, most bees

now placed in *Augochloropsis s. l.* were placed in *Augochlora*. Sandhouse (1937) described *Augochloropsis* in detail and synonymized *Paraugochlora* and *Tetrachlora* with it. Moure (1941a) also noted the characteristics of *Augochloropsis,* considering it a subgenus of *Augochlora*. He later (1943) noted that the designation of type species of *Augochlora* had changed the meaning of *Augochlora* to coincide with *Odontochlora* and not with *Augochloropsis,* and thus raised *Augochloropsis* to the generic level and created a tribe, the Augochloropsini, for it.

The division of *Augochloropsis* into subgenera based on the characters of this study has not previously been recognized. Other generic names now considered to be synonyms of *Augochloropsis s. l.* pertain to the second subgenus, discussed below.

The best known species of *Augochloropsis s. s.* is *A. ignita* (Smith) [senior synonym of *A. subignita* (Cockerell)].

Subgenus **Paraugochloropsis** Schrottky

Augochloropsis (Paraugochloropsis) Schrottky, 1906, Z. Syst. Hymenopter. Dipter. 6:312. (Type species: *Augochloropsis (Paraugochloropsis) lycorias* Schrottky, 1906, monobasic.)

Augochlora (Tetrachlora) Schrottky, 1909, Deut. Entomol. Z. 1909:481. (Type species: *Halictus multiplex* Vachal, 1903, monobasic.)

Paraugochlora Schrottky, 1910, Deut. Entomol. Z. 1910:540. (Type species: *Augochlora spinolae* Cockerell, 1900, original designation.)

Rivalisia Strand, 1921, Arch. Naturgeschichte abt. A, 87:270. (Type species: *Rivalisia metallica* Strand, 1921, monobasic.) NEW SYNONYMY.

Augochlora (Glyptobasis) Moure, 1941, Arq. Zool. Estado São Paulo 2:48. (Type species: *Augochlora (Glyptobasis) chloëra* Moure, 1941a, original designation.) Preoccupied.

Glyptobasia Moure, 1941, Arq. Mus. paranaense 1:98. New name for *Glyptobasis* Moure, preoccupied.

?*Augochloropsis (Glyptochlora)* Moure, 1958, J. New York Entomol. Soc. 66:188. (Type species: *Megalopta ornata* Smith, 1879, original designation.)

Female

(22) Basal area of propodeum smooth, irregularly roughened, or with light plicae, not as described for subgenus *Augochloropsis**.

Male

(36) Distal process of labrum rounded, without median groove (Fig. 152). (39) Metasomal tergum VII with gradulus not notched (Fig. 226). (42) Metasomal sternum IV with long thin lateral processes, clothed with setae to apices, patches of short stout setae anterior to processes (Fig. 244)*. (43) Sternum V with apex not notched, setae not modified, occasionally slightly denser medially. (44) Sternum VI with postgradular flanges little developed (Fig. 247). (45) Sternum VII with truncate or broadly rounded posterior median process (Figs. 293-295). (47) *Ventral gonostylus apically bearing dense unmodified setae* (Fig. 366). (48) *Penis valve with crest of medium height,* as in Fig. 369.

*Exceptions

In a few species, the basal area of the propodeum bears well-impressed striae as in *Augochloropsis s. s.* In one species examined, the lateral projections of metasomal sternum IV are short, and in the type species of *Glyptobasia,* they are essentially absent (Fig. 245).

Paraugochloropsis is much the larger in number of species of the two subgenera and the only one found north of Mexico. I have not been able to study holotypes of the type species of *Paraugochloropsis* or *Paraugochlora,* but their descriptions leave little doubt as to their subgeneric position and specimens in the University of Kansas collection which match their descriptions belong here. *Tetrachlora* appears to be a synonym of *Paraugochloropsis,* judging by specimens of *Augochloropsis euphrosyne* (Holmberg), which according to Schrottky (1909b) is a synonym of the type species of *Tetrachlora, A. multiplex* (Vachal). I have not seen specimens identified as *multiplex,* although the specific description fits specimens of *euphrosyne.*

Rivalisia was proposed for African bees. However, the holotype of the type species is definitely a member of *Paraugochloropsis* and undoubtedly South American in origin. Its systematic position is discussed in Appendix I, under *Augochloropsis metallica* (Strand).

Glyptobasia was described for two coarsely punctate species with unusual propodeal structure (see Moure, 1941a). In addition, both species have a low basal elevation of the female labrum which is only developed in the apical portion of the basal area, with the apical and lateral margins of the basal area high and merging with the elevation. The marginal area of the clypeus is produced between the clypeal teeth. Metasomal sternum IV of the male of *Glyptobasia chloëra* Moure lacks lateral processes (Fig. 245) and the posterior median processes of sterna VII and VIII are low (Fig. 297). However, other characters, especially the genitalia, resemble those of typical *Paraugochloropsis,* and most of the above characteristics are individually found in more typical species of *Augochloropsis,* so I prefer to consider the two species as representing a species group within *Paraugochloropsis.*

Glyptochlora must tentatively be considered a synonym of *Paraugochloropsis* on the subgeneric level, as the male is unknown. I have not seen the type species, but an unidentified female specimen available to me has been compared with the holotype of the type species in the British Museum (Natural History) by Dr. C. D. Michener and found to be congeneric. Moure (1958b) has described the type species in detail; the most noteworthy features are the extremely coarse punctation, the propodeal structure, the sharply ridged vertex behind the ocelli, and the produced and lamellate mesoscutal lip (Fig. 190). The marginal area of the clypeus is produced. As noted by Moure (1958b), the group resembles *Glyptobasia.*

Well known species of *Paraugochloropsis* include *Augochloropsis metallica* (Fabricius) from North America, and *A. vesta* (Smith) and *A. argentina* (Friese) from South America.

Genus **Augochlorodes** Moure

Augochlorodes Moure, 1958, J. Kansas Entomol. Soc., 31:53. (Type species: *Augochlorodes turrifaciens* Moure, 1958a, monobasic and original designation.)

Female

HEAD. (1) Epistomal sulcus forming obtuse angle, as in *Augochloropsis* (Fig. 122). (4) *Preoccipital ridge gradually rounded.* (5, 6) Hypostomal floor longer than wide, l/w = 1.21, c/l = .34 (1 sp.). (8) Inner orbit of compound eye moderately emarginate, as in *Augochloropsis,* w/l = .128 (1 sp.). (11) Labrum (Fig. 150) with short, narrow, triangular distal process; basal elevation suborbicular, rounded, strongly protuberant. (13) Distal portion of maxilla normal, inner strip with broad scale-like cuticular markings and long setae on surface. (14) Maxillary palpus p/M = .48 (1 sp.). (15) Prementum normal, pl/W = .60, pw/pl = .16 (1 sp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa of moderate length, as in *Augochloropsis,* gl/pl = .45, gl/W = .27 (1 sp.).

MESOSOMA. (19) Pronotal lateral angle not produced, obtuse. Dorsal ridge strongly carinate; lateral ridge abruptly rounded. (20) Mesoscutum not narrowed anteriorly, lip rounded. (22) Basal area of propodeum with weak striae basally, smooth apically. (24, 25) *Marginal cell of forewing acute,* stigma enlarged, mc/wl = .60 (1 sp.). (27) *Hind tibial spur pectinate.* (29) Basitibial plate well defined on all edges, narrowly rounded. (30) Anterior basitarsal brush weakly defined.

Male

HEAD. (35) Antenna moderately long, reaching scutellum, no plate areas; sc/2 = 2.46, 2/1 = 1.18, 3/1 = 1.42, 10/1 = 1.57 (1 sp.). (36) Labrum transverse, distal process little developed, basal elevation extending across basal area, not notched.

MESOSOMA. (37) Inner hind tibial spur with long serrations.

METASOMA. (38) Metasoma elongate, not petiolate. (39) Tergum VII abruptly convex apically, posterior surface somewhat flattened, no gradulus. (40) Anal lip of proctiger with short stubby post-anal filaments. (42) *Sternum IV* (Fig. 248) *produced posteriorly at corners of postgradular area, bearing long flattened setae;* gradulus joining antecosta medially. (43) *Sternum V with dense clump of setae medially.* (44) Sternum VI normal, shallowly notched apically. (45) Sternum VII slightly produced posteriorly into truncate lobe, bearing short setae; anteriorly slightly pointed medially, apodemes slightly recurved. Sternum VIII not produced posteriorly, without setae; laterally joining VII at apices of apodemes. Spiculum broad (Fig. 298).

(46) Gonobase (Figs. 375-376) with narrow ventral bridge, dorsal lobes weakly defined. (47) Ventral gonostylus a broad lobe bearing modified setae on its ventral surface, continued anteriorly as thin medially-directed seta-bearing flap. Basal process of gonostylus absent. Dorsal gonostylus a large transparent thin lobe with cuticular wrinkles, continued apically and ventrally as a well-sclerotized hook-like projection and medially as a projection dorsal to the penis valve. (48) Penis valve with ventral prong and dorsal crest, expanded medially and laterally. (49) Volsella truncate basally, inner apical angle produced and projecting ventrally; transverse ridge below notch.

Augochlorodes contains one medium sized (about 7.5 mm) green species, *A. turrifaciens* Moure, nondescript except for the enlarged stigma of the forewing. The bee is weakly punctured with weak propodeal plicae defined only basally and rather resembles species of *Augochlorella* at first glance. The genitalic and sternal structure of the male suggest a relationship with *Augochloropsis*. The female can be distinguished from genera which it resembles by the rounded preoccipital ridge, non-lobed epistomal sulcus, and pectinate tibial spurs; the males are most easily distinguished externally by the fourth and fifth metasomal sterna. The genus is known only from southern Brazil.

Moure (1958a) gives additional characters to distinguish the genus and type species.

Genus **Thectochlora** Moure

Thectochlora Moure, 1941, Arq. Zool. Estado São Paulo 2:51. (Type species: *Halictus alaris* Vachal, 1904a, monobasic and original designation.)

Female

HEAD (Fig. 123). (1) Epistomal sulcus forming obtuse angle. (4) Preoccipital ridge rounded. (5, 6) Hypostomal floor longer than wide, l/w = 1.16, c l = .24 (1 sp.). (8) Inner orbit of compound eye moderately emarginate, w l = .135 (1 sp.). (11) Labrum (Fig. 149) with distal process triangular, narrower than basal area, labral teeth strong; basal elevation rounded and protuberant. (13) Distal portion of maxilla normal, inner strip with broad scale-like cuticular markings and long setae only at apex. (14) Maxillary palpus p M = .35 (1 sp.). (15) Prementum pl W = .62, pw/pl = .20 (1 sp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa rather short, less than half length of prementum, gl pl = .38, gl/W = .24 (1 sp.).

MESOSOMA. (19) *Pronotal dorsal ridge* (Fig. 191) *strongly lamellate, forming flange from lateral angle to lobe*, lateral angle produced and rounded. Lateral ridge rounded. (20) *Mesoscutum produced anteriorly to project over pronotum as lamellate lip.* (22) *Basal area of propodeum short, triangle depressed and striate, otherwise punctate, completely covered with short dense pile.* (23) Posterior surface with long caudally-directed setae. (24, 25) Marginal cell of forewing narrowly truncate, sometimes weakly appendiculate,

mc/wl = .56 (1 sp.). (27) Hind tibial spur pectinate. (29) Basitibial plate poorly defined on anterior edge, narrowly rounded. (30) Anterior basitarsal brush apparently absent.

METASOMA. *Tergum I with anterior surface depressed, flattened, covered with dense short setae, basally dense upward-curved plumose setae enclose an area above petiole, usually containing large mites.* (32) Ridge joining supra-pygidial plate and pygidial plate apparently absent.

Male

HEAD. (35) Antenna long, reaching beyond propodeum, scape short; no plate areas. Flagellomere 2 over twice length of 1, subequal to 10; sc/2 = 1.36, 2/1 = 2.50, 3/1 = 2.14, 10/1 = 2.38 (1 sp.). (36) Labrum transverse, distal process little developed; basal elevation extending across basal area, not notched, as in *Neocorynura* (Fig. 146).

MESOSOMA. (37) *Dorsal surface of middle tibia with dense mat of white pile, obscuring surface.*

METASOMA. (38) Metasoma not elongate, somewhat depressed. (39) Tergum VII rather abruptly convex apically, no gradulus. (40) Anal lip of proctiger without post-anal filaments. (42) *Sternum IV* (Fig. 249) *produced laterally into caudally directed process bearing strong setae at apices; posterior marginal area depressed and shiny centrally, truncate; median patch of short, erect, stout setae on postgradular area.* (43) *Sternum V emarginate, with long plumose setae apically.* (44) Sternum VI normal, weakly notched. (45) Sternum VII not produced posteriorly, bearing fine setae, apodemes strongly recurved. Sternum VIII produced posteriorly into rounded median projection, without setae; laterally joining VII near apices of apodemes. Spiculum narrow (Figs. 299-301).

(46) Gonobase (Figs. 370-374) with narrow ventral bridge, dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus a small medially or apically directed lobe, seta-bearing surface facing anteriorly. Basal process of gonostylus absent; parapenial lobe a thin elongate flap. Dorsal gonostylus an elongate thin flap, projecting medially or anteriorly. (48) Penis valve (Fig. 374) with small ventral prong; thin dorsal crest bordering medial and lateral depressions; valve expanded medially and laterally. (49) Volsella (Fig. 373) rounded basally, apical inner angle slightly produced.

Thectochlora contains one rather unusual medium-sized (about 7 mm) green species, *T. alaris* (Vachal). The mesoscutum and basal area of the propodeum of the female are covered with short dense pile. The female is most unusual in the modification of the first metasomal tergum to form an acarinarium. The green male with orange tibiae and whitish basitarsi can be distinguished externally from other genera by the pronotal and mesoscutal structure, patch of dense pile on the second tibiae, and the externally visible

metasomal sterna. Specimens have been seen from southern Brazil, Paraguay and Argentina.

Moure (1941a) gave additional characteristics of the genus and illustrated the fourth metasomal sternum of the male.

Genus **Augochlora** Smith

Female

HEAD. (Figs. 125-126). (1) *Epistomal sulcus forming acute angle, epistomal lobe protruding into clypeus.* (2) *Clypeus relatively flat, green almost to apex.* (4) Preoccipital ridge carinate. (5, 6) Hypostomal floor, l/w = 1.90 to 2.50, c l = .30 to .54 (17 spp.). (7) *Anterior angle of hypostomal carina usually forming sharp right angle or produced into spine.* (8) Inner orbit of compound eye deeply emarginate, w/l = .120 to .168 (18 spp.)*. (11) Distal process of labrum triangular, not narrowed, as long or longer than basal area (Figs. 153, 155, 156). Basal elevation variable, see subgeneric descriptions. (12) Mandible normal, elongate, or bidentate, see subgeneric descriptions. (13) Distal portion of maxilla normal, of moderate length (Fig. 175). Inner strip with narrow scale-like cuticular markings and setae on surface of strip (Fig. 175). (14) Maxillary palpus, p/M = .28 to .39 (27 spp.).

MESOSOMA. (19) Pronotal lateral angle usually slightly produced, forming acute or occasionally obtuse angle (Fig. 192)*. Lateral ridge sharply angled, rarely rounded; dorsal ridge carinate. (20) Mesoscutum not narrowed anteriorly, lip rounded, frequently high*. (22) Basal area of propodeum striate or rugose, sometimes finely so with striae not reaching posterior margin. (24) *Marginal cell of forewing truncate, usually appendiculate,* mc/wl = .52 to .61 (17 spp.). (27) *Hind tibial spur with rounded serrations, basal area raised* (Fig. 214). (29) Basitibial plate well defined on all edges, with distinct rim, narrowly or broadly rounded apically. (30) Anterior basitarsal brush present.

METASOMA. (31) Pseudopygidial area of tergum V normal or with scale-like setae (Fig. 223). (33) *Sternum I normal or produced into median ridge, tubercle, or spine* (Fig. 225). (34) Sternum IV with gradulus (Fig. 250), rarely weakly defined. Sterna and terga otherwise normal.

Male

HEAD. (35) Antenna (Fig. 179) moderately long, no plate areas; sc/2 = 3.20 to 4.90, 2/1 = .82 to 1.75, 3/1 = 1.05 to 2.18, 10/1 = 1.50 to 3.18 (12 spp.)*. (36) Labrum (Fig. 154) with distal process well developed, triangular, subequal in length to basal area; basal elevation extending across basal area, not notched medially.

METASOMA. (39) Tergum VII sharply convex apically, gradulus not defined*. (40) Anal lip of proctiger (Fig. 236) with post-anal filaments. (42-44) Sterna IV to VI (Figs. 251-253) usually normal. Apical margin of VI entire or

weakly notched. (45) Sterna VII and VIII with posterior margins variously produced medially, not bilobed, with or without setae. Apodemes of VII strongly recurved anteriorly. Spiculum narrow. Sternum VIII laterally joining VII far from tips of apodemes (Figs. 302-306).

(46) Gonobase (Figs. 377-383) with narrow ventral bridge, dorsal lobes wide, strongly projecting over gonocoxites. (47) Ventral gonostylus an elongate flattened lobe, with seta-bearing surface facing ventrally; ridge lateral to ventral gonostylus continued dorsally, bearing setae. Basal process of gonostylus present, bearing setae. Dorsal process of gonostylus a simple continuation of lateral ridge. (48) Penis valve (Fig. 379) with ventral prong, without dorsal crest, expanded laterally. (49) Volsella (Fig. 380) quadrate.

*EXCEPTIONS

In macrocephalic specimens with enlarged genal areas, the eyes are weakly notched, w/l = .083 to .110 (4 spp.). In two species, the lateral angle of the pronotum is strongly produced (Fig. 194), with the mesoscutum narrowed anteriorly and its lip high and sharply angled or carinate. In one male, the antennae are long and bear plate areas, sc/2 = 1.88. In another male, a gradulus is weakly defined on metasomal tergum VII.

Most *Augochlora* are medium-sized to large bright green bees, although many species are partially or wholly black. The genus is very large, with species from Canada to Argentina. *Augochlora* can be divided into two poorly separated large subgenera and one quite distinct small subgenus. Separation of the former two subgenera is significant principally for biological reasons, as will be described in more detail in a later paper (Eickwort, in preparation).

Subgenus **Augochlora** Smith

Augochlora Smith, 1853. Catalogue of hymenopterous insects in the collection of the British Museum, 1:73. (Type species: *Halictus purus* Say, 1837, designated by Cockerell, 1923.)
Odontochlora Schrottky, 1909, Rev. Mus. La Plata 16:141. (Type species: *Augochlora muelleri* Cockerell, 1900, original designation.)
Oxystoglossa Smith, 1853, Catalogue of hymenopterous insects in the collection of the British Museum 1:83. (Type species: *Oxystoglossa decorata* Smith, 1853, monobasic.)

Female

(1) Epistomal lobe deeply protruding into clypeus. (2) Apex of clypeus normal. (11) Labrum (Fig. 153) with distal process not as wide as basal area; basal elevation transverse, strongly protuberant and rounded. (12) Mandible (Fig. 163) with apex bidentate, subapical tooth produced, outer posterior ridge frequently swollen. (15) Prementum normal, of moderate length and width (Fig. 170), pl/W = .67 to .86, pw/pl = .13 to .21 (13 spp.). (16) Salivary plate normal, V-shaped brace, or well sclerotized without defined brace when glossa very long. (17) *Glossa long to very long, over half as long as prementum*, gl/pl = .58 to .98, gl/W = .39 to .84 (14 spp.)*. (18) Palpal

segments 2 plus 3 subequal to or shorter than 1. (19) Lateral angle of pronotum usually produced and acute, sometimes obtuse. (29) Basitibial plate broadly rounded. (31) *Pseudopygidial area with scale-like setae bordering median slit.* (33) Sternum I with or without median ridge, tubercle, or spine.

Male

(39) Apex of metasomal tergum VII normal. (43-44) Sterna V and VI normal. (45) Sternum VII (Fig. 303) without spiculum-like median anterior sclerotized apodeme. (47) Lateral ridge bordering ventral gonostylus of genitalia (Fig. 377) with short setae. Ventral gonostylus a narrow lobe with unmodified setae, as in Fig. 377. (48) Penis valve without strong lateral extensions joined by dorsal ridge.

*Exception

In one species with an exceptionally long head, the prementum and glossa are also exceptionally long, pl W = 1.04, gl/pl = 1.71, and gl/W = 1.79.

Females of *Augochlora s. s.* are most readily placed in this subgenus by the bidentate mandibles and normal truncate clypeus. The spine on the first metasomal sternum is frequently absent. Species of *Augochlora s. s.* tend to be bluish-green or partially or wholly black, in contrast to most *Oxystoglossella.*

Smith's (1853) original *Augochlora* included many diverse augochlorine bees, characterized by bright green coloration and deeply emarginate eyes. Many of Smith's *Augochlora* species are today considered *Augochloropsis,* and the name *Augochlora* was usually reserved by early authors for bees today placed in that genus. Schrottky (1909a) named *Odontochlora* for those species with a simple tibial spur and spined first metasomal sternum, and he (1909b) widened *Oxystoglossa* to include similar species without an armed first sternum. Although Vachal (1911) rejected this separation, *Odontochlora* and *Oxystoglossa* were widely used to include species now placed in *Augochlora,* until Cockerell (1923) designated *Augochlora pura* (Say), a species of *Odontochlora,* as type species of *Augochlora.* Sandhouse (1937) synonymized *Odontochlora* and *Oxystoglossa* with *Augochlora* and correctly described the genus, distinguishing it from *Augochloropsis.*

Smith (1853) named *Oxystoglossa* for one Jamaican species, *decorata,* similar to *Augochlora* but with a greatly elongated glossa. Dr. I. H. H. Yarrow of the British Museum (Natural History) kindly loaned the type specimen (a female) of *O. decorata* to me for examination. It is in poor condition and some pertinent characters could not be observed. I place it in *Augochlora s. s.* on the basis of scale-like setae bordering the pseudopygidial median slit and mandibles which more closely resemble those of species of *Augochlora* than of *Oxystoglossella.*

All species of *Augochlora s. s.* which have been investigated biologically

have been found to nest in wood. This large subgenus includes such species as *Augochlora pura* (Say) (North America), *A. nigrocyanea* Cockerell and *A. smaragdina* Friese (Mexico and Central America), and *A. esox* (Vachal) and *A. muelleri* Cockerell (South America).

Subgenus **Oxystoglossella,** new subgenus

(Type species: *Augochlora cordiaefloris* Cockerell, 1907.)

Female

(1) Epistomal lobe deeply protruding into clypeus. (2) Apex of clypeus normal. (11) Labrum (Fig. 156) with distal process not as wide as basal area; basal elevation suborbicular, strongly protuberant and rounded*. (12) Mandible normal*. (15) Prementum normal, of moderate length and width, pl/W = .70 to .89, pw/pl = .14 to .18 (10 spp.). (16) Salivary plate normal with V-shaped brace, or well sclerotized without defined brace when glossa very long. (17) *Glossa usually long, usually over .75 as long as prementum,* gl/pl = .71 to .92, gl/W = .53 to .79 (10 spp.). (18) Palpal segments 2 plus 3 equal to or shorter than 1. (19) Lateral angle of pronotum usually produced and acute, occasionally obtuse. (29) Basitibial plate usually narrowly rounded, occasionally broadly rounded. (31) No scale-like setae on pseudopygidial area. (33) Sternum I usually normal, rarely with slight median ridge or tooth.

Male

(39) Apex of metasomal tergum VII normal. (43, 44) Sterna V and VI normal. (45) Sternum VII (Fig. 305) without spiculum-like median anterior sclerotized apodeme. (47) Lateral ridge bordering ventral gonostylus with very long setae, surpassing gonostylus (Fig. 381). Ventral gonostylus a narrow lobe with unmodified setae, as in *Augochlora s. s.* (48) Penis valve without lateral extensions joined by dorsal ridge.

*Exceptions

In four species examined, the females are highly polymorphic in head size, as described by Sakagami and Moure (1965) for *Augochlora semiramis* (Schrottky). The macrocephalic individuals have greatly expanded genae and vertices and shallowly emarginate eyes. In these, the basal elevation of the labrum tends to be very low and transverse, and the distal process as wide as the basal area, and the mandibles are greatly elongated (Fig. 164). The male antennae of one species of this group are exceptionally long and bear plate areas, as mentioned in the exceptions to the generic description.

Members of *Oxystoglossella* closely resemble *Augochlora s. s.,* but are usually more yellowish-green, rarely black, although there is wide color overlap. Females are best separated by mandibular characteristics; males cannot readily be separated from *Augochlora s. s.* without dissection. Revisionary

studies of *Augochlora s. l.* may lead to synonymizing *Oxystoglossella* with *Augochlora s. s.* Both subgenera contain many species; *Oxystoglossella* barely reaches southwestern United States while *Augochlora s. s.* ranges into Canada.

Species of *Oxystoglossella* have previously been placed in *Oxystoglossa*, but subgenerically *Oxystoglossa* appears to be synonymous with *Augochlora s. s.*, based on examination of the type species. I have selected a well known and easily recognizable Mexican and Central American species whose nest structure is known (Eickwort and Eickwort, in preparation) as type species of *Oxystoglossella*.

All species of *Oxystoglossella* which have been investigated biologically have been found to be soil-nesting. This subgenus includes such species as *Augochlora aztecula* Cockerell and the *A. clarki* Michener group (Michener, 1954) (Mexico and Central America), and *A. thalia* Smith (South America).

Subgenus **Mycterochlora,** new subgenus
(Type species: *Halictus repandirostris* Vachal, 1911.)

Female

(1) Epistomal sulcus forming an angle only slightly more acute than a right angle, epistomal lobe not deeply protruding into clypeus. (2) *Apex of clypeus prolonged beyond marginal area, rounded and slightly upturned, covering half of labral basal area.* (11)Distal process of labrum (Fig. 155) as broad as basal area; basal elevation transverse, on apical half of basal area only. (12) Mandible bidentate at apex, subapical tooth produced as in *Augochlora s. s.*, outer posterior ridge not swollen. (15) Prementum normal, comparatively shorter and wider, pl W = .54 to .56, pw/pl = .22 to .25 (3 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa comparatively shorter, about half as long as prementum, gl/pl = .43 to .50, gl/W = .23 to .27 (3 spp.). (18) Palpal segments 2 plus 3 longer than 1. (19) Lateral angle of pronotum not produced, forming obtuse angle (Fig. 193). (29) Basitibial plate very broadly rounded. (31) Pseudopygidial area of metasomal tergum V with scale-like setae bordering median slit, as in *Augochlora s. s.* (33) Sternum I not armed.

Male

(39) Apex of metasomal tergum VII flanged outwards, appearing carinate. (43, 44) Sterna V and VI with strong depressions apically, bordered by row of strong setae on VI and with median ridge at base of concavity on V, small acrosternite present on VI. (45) Sternum VII (Fig. 306) with short well-sclerotized median anterior apodeme, homologous in position with spiculum of VIII but joined by membrane to VII. Spiculum on VIII normal. (47) Lateral ridge bordering ventral gonostylus (Fig. 382) very narrow, with short setae. Ventral gonostylus a broad flat lobe with short stout setae near

apex. (48) Penis valve (Fig. 383) with lateral extensions joined by V-shaped dorsal ridge.

Mycterochlora is a distinctive subgenus of two or three species known from Brazil, Peru, Bolivia, Colombia, and Guyana. The females are quite different in general appearance from *Augochlora s. s.,* with femora, tibiae, and basitarsi broadened and densely clothed with setae. The legs of the males are also broad. Females can easily be recognized by the clypeus. The male of *Augochlora repandirostris* is easily distinguished by the testaceous last visible metasomal tergum with a produced carinate margin, contrasting strongly with the other dark brown terga. I have not seen males of other species.

While this group has never been recognized formally, Vachal (1911) noted the unique condition of the female clypeus and described two species, *Halictus repandirostris* and *H. pachytes,* in the *Halicti falcati.* I have not seen the types of either species, but a series available to me agrees exactly with the description of *Augochlora repandirostris* (Vachal) and forms the basis for the subgeneric description.

Derivation of *Mycterochlora:* Beak or nose, plus root (reference to *Augochlora*), in reference to the clypeus of the female (feminine).

Genus **Augochlorella** Sandhouse

Augochlorella Sandhouse, 1937, J. Washington Acad. Sci. 27:66. (Type species: *Augochlora gratiosa* Smith, 1853, original designation.)

Oxystoglossidia Moure, 1943, Rev. Entomol. (Rio) 14:473. (Type species: *Oxystoglossidia uraniella* Moure, 1943, original designation.)

Female

HEAD (Fig. 127). (1) *Epistomal sulcus forming right angle.* (4) Preoccipital ridge sharply angled or weakly carinate. (5, 6) Hypostomal floor, l/w = 1.33 to 1.49; c/l = .13 to .38 (4 spp.). (8) Inner orbit of compound eye deeply emarginate, w/l = .134 to .159 (4 spp.). (11) Labrum (Fig. 157) with distal process triangular, usually narrower than basal area; basal elevation suborbicular to transverse, rounded and protuberant*. (13) Distal portion of maxilla normal, inner strip with narrow scale-like cuticular markings and setae on edge of strip. (14) Maxillary palpus, p/M = .33 to .43 (6 spp.). (15) Prementum normal, pl/W = .65 to .79, pw/pl = .17 to .20 (6 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa about half length of prementum, gl/pl = .46 to .60, gl/W = .30 to .47 (6 spp.).

MESOSOMA. (19) Pronotal lateral angle not produced, forming obtuse or right angle*. Dorsal ridge strongly carinate; lateral ridge sharply angled. (20) Mesoscutum not narrowed anteriorly, lip usually broadly rounded*. (22) Basal area of propodeum striate or rugose, striae occasionally not reaching posterior margin, not granular. (24, 25) *Marginal cell of forewing acute* (Fig. 20), rarely narrowly truncate, mc/wl = .54 to .61 (4 spp.). (27) *Hind*

tibial spur with rounded serrations, basal area raised, as in *Augochlora* (Fig. 214). (29) Basitibial plate well-defined on all edges, narrowly rounded. (30) Anterior basitarsal brush poorly defined.

Male

HEAD. (35) Antenna moderately long, flagellomere 2 very short, much wider than long; no plate areas; sc 2 = 4.89 to 5.88, 2 1 = .76 to .95, 3/1 = 1.09 to 1.10, 10/1 = 2.09 to 2.73 (3 spp.). (36) Labrum with distal process well developed, triangular, usually shorter than basal area; basal elevation extending across basal area, not notched medially; similar to *Augochlora* (Fig. 154).

METASOMA. (39) Tergum VII sharply convex apically, gradulus not or weakly defined. (40) Anal lip of proctiger with post-anal filaments. (42-44) Sterna IV to VI normal, not modified. Apical margin of VI notched, slight median longitudinal ridge sometimes present. (45) Sternum VII variously produced posteriorly, not bilobed, usually with setae; apodemes slightly recurved. Sternum VIII not or slightly produced posteriorly; usually without apical setae; laterally joining VII at apices of apodemes. Spiculum narrow (Figs. 307-309).

(46) Gonobase (Figs. 384-387) with narrow ventral bridge, dorsal lobes strongly or weakly projecting over gonocoxites. (47) Ventral gonostylus of two parts, a posterior-lateral, rounded, seta-bearing lobe and an inner lobe bearing row of flattened modified setae on margin; inner lobe variously shaped, often long and narrow. Basal process of gonostylus absent. Dorsal gonostylus a variously shaped membranous flap projecting from inner edge of ridge, occasionally a long thin flap reaching midline. (48) Penis valve (Fig. 387) with ventral prong; without dorsal crest but with median dorsal ridge bordering depression on inner side; variously expanded laterally and medially. (49) Volsella (Fig. 386) pointed basally, triangular below notch.

*Exceptions

In *Augochlorella edentata* Michener, the female labrum resembles that of *Pereirapis* (Fig. 158), the teeth on the distal process being very strong and the basal elevation apical and very low. In one species observed, the pronotal lateral angles are somewhat produced and the mesoscutal lip rather high. In one male, the antennae are exceptionally short, 2 1 = .46, 3 1 = .51, and 10/1 = 1.91.

Species of *Augochlorella* are usually bright green, medium to small in size, and closely resemble many species of *Augochlora (Oxystoglossella)*, from which they can be distinguished by the epistomal sulcus and marginal cell apex. The male genitalia in particular justify regarding *Augochlorella* as a separate genus. *Augochlorella* is distinguished from the closely related

Pereirapis and *Ceratalictus* in discussions of these genera. *Augochlorella edentata* Michener, considered somewhat intermediate between *Pereirapis* and *Augochlorella* by Ordway (1966), is a true *Augochlorella,* intermediate only in its small size and female labrum. About 15 species of *Augochlorella* have been recorded (Ordway, 1966), from Canada to Argentina.

Sandhouse (1937) named *Augochlorella* for four species of North American bees and described the genus in detail, differentiated it from *Augochlora* and *Augochloropsis,* provided a key and descriptions of the North American species, and illustrated the genitalia. Michener (1944, 1951) at first considered *Augochlorella* to be a subgenus of *Augochlora,* but later (1954) returned it to generic rank. Moure (1943) named *Oxystoglossidia* for two South American species, not having seen Sandhouse's paper. After obtaining the paper and specimens of the type species of *Augochlorella,* he (Moure, 1944a) synonymized *Oxystoglossidia* with *Augochlorella.*

Ordway (1966) has recently revised the eight North American and Mexican species of *Augochlorella.* She presented diagnostic characters for the genus, separated it from other North American (north of Mexico) green halictid genera and illustrated the male genitalia and hidden sterna and terga of North American *Augochlorella.*

Well known species of *Augochlorella* include *A. striata* (Provancher) from North America, *A. pomoniella* (Cockerell) from the United States, Mexico, and Central America, and *A. urania* (Smith) from South America.

Genus **Ceratalictus** Moure

Ceratalictus Moure, 1943, Rev. Entomol. (Rio) 14:463. (Type species, *Oxystoglossa theia* Schrottky, 1911, original designation.)

Female

HEAD (Fig. 124). (1) *Epistomal sulcus forming obtuse angle.* (4) Preoccipital ridge carinate. (5, 6) Hypostomal floor longer than wide, l/w = 1.11, c/l = 0 (1 sp.). (8) Inner orbit of compound eye deeply emarginate, w/l = .154 (1 sp.). (11) Labrum with distal process triangular, basal elevation suborbicular, protuberant, as in *Augochlorella* (Fig. 157). (13) Distal process of maxilla normal, inner strip with narrow scale-like cuticular markings. (14) Maxillary palpus, p/M = .40 (1 sp.). (15) Prementum normal, pl/W = .57, pw/pl = .25 (1 sp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa rather short, gl/pl = .30, gl/W = .17 (1 sp.).

MESOSOMA. (19) Pronotal lateral angle produced, forming acute angle. Dorsal ridge carinate; lateral ridge sharply angled. (20) Mesoscutum not narrowed anteriorly, lip high and rounded. (22) Basal area of propodeum striate. (24, 25) *Marginal cell of forewing acute or very narrowly truncate,* mc/wl = .54 (1 sp.). (27) *Hind tibial spur* (Fig. 215) *with rounded serrations, basal area not raised.* (29) Basitibial plate poorly defined on anterior

edge, narrowly rounded or pointed. (30) Anterior basitarsal brush poorly defined.

METASOMA. (31-34) Terga and sterna normal, sternum IV with gradulus defined basally.

Male

HEAD. (35) Antenna moderately long, flagellomere 2 not narrowed, almost as long as wide; no plate areas, sc 1 = 2.85, 2 1 = .98, 3/1 = 1.25, 10/1 = 1.79 (1 sp.). (36) Labrum with distal process well developed, triangular, basal elevation extending across basal area, not notched medially; similar to *Augochlora* (Fig. 154).

METASOMA. (39) Tergum VII sharply convex apically, gradulus not defined. (40) Anal lip of proctiger without post-anal filaments (Fig. 233). (42-44) Sterna IV to VI normal, not modified, as in *Augochlorella*. Apical margin of VI weakly notched. (45) Sternum VII not produced posteriorly, apodemes bent strongly anteriorly. Sternum VIII medially produced, apices VII and VIII bear setae. Sternum VIII laterally joins VII far from apodemes. Spiculum narrow (Figs. 310-312).

(46) Gonobase (Figs. 388-392) with narrow ventral bridge, dorsal lobes wide and strongly projecting over gonocoxites. (47) Ventral gonostylus of two parts, a posterior-lateral rounded seta-bearing lobe and a large lobe with seta-bearing surface facing inward (Fig. 391). Small membranous parapenial lobe present; basal process of gonostylus present, bearing setae. Dorsal gonostylus a long thin transparent flap, reaching midline. (48) Penis valve (Fig. 390) with small ventral prong, longitudinal dorsal ridge apical to dorsal depression, valve slightly expanded laterally. (49) Volsella (Fig. 392) with notch near base, base almost truncate.

The two described species of *Ceratalictus* are medium-sized green bees very closely resembling *Augochlorella*. The difference between *Ceratalictus* and that genus center primarily in the male hidden sterna and terga and the genitalia, and it is a matter of choice whether *Ceratalictus* should be given separate generic status or considered a subgenus of *Augochlorella*. Females of *Ceratalictus* can be distinguished with difficulty from *Augochlorella* by the obtusely angled epistomal sulcus and the tibial spur. Males without dissection are also difficult to distinguish; the antennae, entirely green clypeus (yellow-margined in *Augochlorella*), and more narrowly elongate metasoma are aids. Moure (1950) gave other characteristics to separate *Ceratalictus* from the species of *Augochlorella* and *Pereirapis* occurring in its range. *Ceratalictus* is known from southern Brazil, Paraguay, Bolivia and Argentina.

Moure (1943) named *Ceratalictus* in a key, but did not describe it fully until later (Moure, 1950), when he was able to associate the sexes. He then separated it in a key from related genera and named a second species, *C. allostictus* Moure.

Genus **Pereirapis** Moure

Pereirapis Moure, 1943, Rev. Entomol. (Rio) 14:461. (Type species: *Pereirapis rhizophila* Moure, 1943, original designation.)

Female

HEAD. (1) *Epistomal sulcus forming right or slightly obtuse angle.* (4) Preoccipital ridge sharply angled or carinate. (5, 6) Hypostomal floor longer than wide, l/w = 1.20 to 1.42, c/l = .12 to .34 (3 spp.). (8) Inner orbit of compound eye deeply emarginate, w/l = .125 to .168 (3 spp.). (11) *Labrum* (Fig. 158) *with distal process triangular, projecting laterally from beneath triangular basal area, teeth between fimbria long; basal elevation apical and low.* (13) Distal portion of maxilla normal, inner strip with narrow scale-like cuticular markings. (14) Maxillary palpus, p/M = .39 to .41 (3 spp.). (15) Prementum normal, pl/W = .65 to .70, pw/pl = .18 to .20 (3 spp.). (16) Salivary plate normal, V-shaped brace. (17) Glossa less than half length of prementum, gl/pl = .34 to .42, gl/W = .49 to .55 (3 spp.).

MESOSOMA. (19) Pronotal lateral angle not produced, forming obtuse or right angle*. Dorsal ridge carinate; lateral ridge sharply angled*. (20) Mesoscutum not narrowed anteriorly, lip broadly rounded. (22) *Basal area of propodeum striate basally, strongly granular, long.* (24, 25) *Marginal cell of forewing acute,* mc/wl = .49 to .55 (3 spp.). (27) *Hind tibial spur with few short rounded teeth, basal tooth largest* (Fig. 216). (29) Basitibial plate well defined on all edges, narrowly rounded. (30) Anterior basitarsal brush apparently absent.

METASOMA. (31-34) Terga normal, setae sparse bordering median slit of pseudopygidial area. Sterna IV and usually V with gradulus defined basally.

Male

HEAD. (35) Antenna moderately long, no plate areas, sc/2 = 3.36 to 4.61, 2/1 = .70 to 1.08, 3/1 = 1.19 to 1.53, 10/1 = 1.80 to 2.19 (4 spp.). (36) Labrum with distal process well developed, triangular, usually shorter than basal area; basal elevation extending across basal area, not notched medially; similar to *Augochlora* (Fig. 154).

METASOMA. (39) Tergum VII sharply convex apically, gradulus not or weakly defined. (40) Anal lip of proctiger without post-anal filaments. (42) *Sternum IV* (Fig. 254) *emarginate apically, with posterior-lateral clumps of long flattened setae,* similar setae occasionally also on postgradular area. (43, 44) Sterna V and VI normal, apical margin of VI (Fig. 255) produced medially and notched, dorso-lateral areas of VI wide. (45) Sternum VII not produced medially and projecting beyond sternum VIII, usually bearing setae. Sternum VIII slightly produced medially, bearing few or no setae, joining VII laterally before apices of apodemes*. Spiculum narrow (Fig. 313).

(46) Gonobase (Figs. 393-396) with narrow ventral bridge, dorsal lobes wide and strongly projecting over gonocoxites. (47) Ventral gonostylus of two parts, a posterior-lateral lobe bearing setae and an apically directed inner lobe bearing unmodified setae on its ventral surface. Basal process of gonostylus present, bearing setae*. Dorsal gonostylus a thin, transparent, medially directed flap bearing a darkly pigmented strip*. (48) Penis valve (Fig. 395) without well-developed ventral prong; without dorsal crest but with median longitudinal ridge; expanded medially and laterally*. (49) Volsella (Fig. 396) rounded basally, notch near apex*.

*Exceptions

A unique male specimen from Brazil differs significantly from typical *Pereirapis* in several respects. The pronotal lateral angle is produced and acute, and the lateral ridge carinate. The propodeum (male) is weakly roughened basally and shiny posteriorly. Sternum VIII joins VII at the apices of the apodemes and VII is not strongly curved anteriorly. The basal process of the gonostylus is absent. The dorsal gonostylus is basically typical of the genus but greatly expanded, reaching the midline. The penis valve appears to bear a ventral prong. The volsella is notched medially and appears to be prolonged basally, not rounded.

Species of *Pereirapis* seen by me are very small (about 5 mm) and green with the metasoma usually largely brown. The genus is closely related to *Augochlorella*, separated principally on male metasomal and genitalic characters. The females of *Pereirapis* can be separated from those of *Augochlorella* by the tibial spurs, labrum, granular long propodeum, and usually smaller size; *Augochlorella edentata* Michener is the same size as *Pereirapis* and bears a similar labrum. Males are difficult to distinguish externally from *Augochlorella;* the abdomen is more narrowly elongate, and the bees are smaller than most *Augochlorella*. Dissection reveals the modified fourth metasomal sternum and different genitalia. *Pereirapis* is a rather small genus with about seven species (Moure, in Ordway, 1966) recorded from Mexico to Brazil.

Moure (1943) named *Pereirapis* for a Brazilian species, and separated it from *Augochlorella* (calling the latter *Oxystoglossidia*) in a key. He gave further separating characters in a later key (Moure, 1950) to the *Halicti falcati* of Vachal. Michener (1954) synonymized *Pereirapis* with *Augochlorella*. Ordway (1966) thought that *Pereirapis* represents a legitimate group and perhaps should be recognized at the subgeneric level in *Augochlorella*.

Genus **Pseudaugochloropsis** Schrottky

Augochloropsis (*Pseudaugochloropsis*) Schrottky, 1906, Z. Syst. Hymenopter. Dipter. 6:313. (Type species: *Halictus nigromarginatus* Spinola, 1851, designated by Schrottky, 1909b.)
Caenaugochlora (*Pseudaugochlora*) Michener, 1954, Bull. Amer. Mus. Natur. Hist. 104:77. (Type species: *Halictus nigromarginatus* Spinola, 1851, original designation.)

Female

HEAD. (1) Epistomal sulcus forming right angle. (4) *Preoccipital ridge rounded, vertex produced to rounded ridge above ocelli* (Fig. 3). (5, 6) Hypostomal floor over 1.5 times longer than wide, l/w = 1.84 to 2.10, c/l = .40 to .43 (2 spp.). (7) Posterior flange projects beyond occiput (Fig. 4). (8) Inner orbit of compound eye strongly emarginate, w/l = .139 to .186 (3 spp.). (11) Labrum with distal process triangular, narrower than basal area; basal elevation suborbicular, strongly protuberant with apical face flattened (Figs. 7-8). (13) *Distal portion of maxilla with apex of galea pointed, well-sclerotized* (Fig. 21), inner strip with narrow scale-like cuticular markings and surface with long setae. Maxilla (Figs. 19-20) long and slender. (14) Maxillary palpus, p/M = .29 to .31 (3 spp.). (15) *Prementum* (Figs. 23-25) *with anterior surface flattened, premental thickenings absent,* long and slender, pl/W = .64 to .72, pw/pl = .11 (3 spp.). (16) Salivary plate (Fig. 27) well sclerotized, V-shaped brace not apparent. (17) *Glossa very long,* gl/pl = .68 to .75, gl/W = .46 to .50 (3 spp.). (18) Labial palpus with segment 1 flattened, longer than 2 plus 3.

MESOSOMA. (19) Pronotal lateral angle not produced, obtuse (Fig. 32). Dorsal ridge strongly carinate; lateral ridge rounded. (20) Mesoscutum not narrowed anteriorly, lip broadly rounded. (22) Basal area of propodeum with anastomosing rugae. (24, 25) Marginal cell of forewing (Fig. 37) narrowly truncate and appendiculate, mc/wl = .58 to .62 (3 spp.). (27) *Hind tibial spur pectinate* (Fig. 53). (29) Basitibial plate narrowly rounded, all edges defined (Fig. 46). (30) Anterior basitarsal brush well defined (Fig. 50).

Male

HEAD. (35) *Antenna moderately long, terminal flagellomere hooked* (Fig. 79), plate areas present or absent. Scape short, flagellomeres 2-10 nearly equal, much longer than 1; sc/2 = 2.25 to 2.89, 2/1 = 1.72 to 2.54, 3/1 = 1.69 to 2.49, 10/1 = 1.85 to 2.86 (3 spp.). (36) Labrum (Fig. 81) with distal process well developed, triangular; basal elevation notched medially, located only centrally.

METASOMA. (39) Tergum VII (Figs. 94-95) abruptly convex apically, gradulus present or absent. (40) Anal lip of proctiger (Fig. 96) with post-anal filaments. (42) *Sternum IV* (Fig. 101) *with modified apical margin depressed posterior to strong ridge, bearing distinctive lateral or median tufts of long setae.* (43) *Sternum V* (Fig. 102) *with modified apical margin, usually bearing lateral tufts of setae, postgradular area variously ridged and depressed.* (44) Sternum VI (Fig. 103) strongly depressed apically, notched medially. (45) Sternum VII with posterior-lateral corners strongly produced and pointed, apodemes recurved anteriorly. Sternum VIII with truncate or rounded median posterior projection bearing long, strong setae; laterally joining VII far from apodemes. Spiculum moderately broad (Figs. 104-106).

(46) Gonobase (Figs. 107-111) with narrow or membranous ventral bridge, dorsal lobes slightly produced. (47) Ventral gonostylus a caudally directed seta-bearing lobe, with thickened setae on inner edge. Parapenial lobe a thin transparent flap; basal process of gonostylus absent. Dorsal gonostylus with long setae above gonocoxite, produced into ventrally-facing flattened surface, medial to and more or less above ventral gonostylus. (48) Penis valve (Fig. 111) without ventral prong, with strong, darkly pigmented crest apical to dorsal depression. (49) Volsella (Fig. 110) emarginate on inner edge, notch near apex, base not narrowed.

Pseudaugochloropsis is a small but widespread genus of moderately large to large bees. Most species are green, although some have black forms (Eickwort, 1967) or are partly reddish. In females, the mesoscutum is distinctly punctate, the propodeal basal area completely rugose, the supraclypeal area sharply beveled, and the head distinctly wider than long with a pronounced ridge above the ocelli. Males are quickly distinguished by the hooked antennae; the setal patterns on sterna IV and V vary but are usually recognizable as modifications of the type illustrated. *Pseudaugochloropsis* appears to be related to *Caenaugochlora*, from which it is distinguished in the discussion of that genus. Species of *Pseudaugochloropsis* are known from Texas to Argentina.

Schrottky (1906) named *Pseudaugochloropsis* for the *Halicti sericei* of Vachal, characterizing it simply as *Augochloropsis* without setal borders ("Haarbinden") on the apical margins of the abdominal segments. At the time he mentioned only two species specifically, both of them described as new. He later (Schrottky, 1909b) designated *Augochlora nigromarginata* (Spinola) as type species, a species which he did not specifically mention in 1906, but which was in the *Halicti sericei* and therefore included by implication. Sandhouse (1937) considered this designation invalid and designated *Augochloropsis sthena* Schrottky, described as a new species in *Pseudaugochloropsis* in 1906, as type species. However, *A. sthena* is a true *Augochloropsis*, as pointed out by Michener (1954). Moure (1944a) disagreed with Sandhouse, pointing out that Schrottky named his subgenus for the *Halicti sericei*, to which *Halictus nigromarginatus* belongs.

Moure (1941a) first accurately characterized *Pseudaugochloropsis*, restricting it to *nigromarginatus*. Most species previously placed in *Pseudaugochloropsis* actually belong in *Augochloropsis*.

Michener (1954) followed Sandhouse's designation of type species and thus synonymized *Pseudaugochloropsis* with *Augochloropsis*. He created the name *Pseudaugochlora* to replace *Pseudaugochloropsis* as used by Moure, and recognized its relation to *Caenaugochlora* by making it a subgenus of the latter. Moure (1946) again argued for the validity of *Pseudaugochloropsis* in

the present sense, a view which Michener has since accepted (see Michener and Kerfoot, 1967).

The only well-known species of *Pseudaugochloropsis* is *P. graminea* (Fabricius), synonymous with *P. nigromarginatus* (see Moure, 1960b).

Genus **Caenaugochlora** Michener

Female

HEAD. (1) *Epistomal sulcus forming right angle.* (4) *Preoccipital ridge sharply angled or carinate**. (5,6) Hypostomal floor longer than wide, l/w = 1.12 to 1.76, c/l = 0 to .59 (3 spp.). (8) Inner orbit of compound eye strongly emarginate, w/l = .123 to .173 (6 spp.). (11) Labrum with distal process triangular, narrower than basal area; basal elevation suborbicular to elongate, strongly protuberant; see subgeneric descriptions. (12) Mandible normal*. (13) Distal portion of maxilla normal, inner strip with narrow scale-like cuticular markings and long setae on edge. (14) Maxillary palpus, p/M = .33 to .44 (8 spp.). (15) Prementum normal, pw/pl = .17 to .19, pl/W = .64 to .86 (9 spp.). (16) Salivary plate well sclerotized, V-shaped brace not apparent*. (17) Glossa long to very long, usually over 1/2 length of prementum, gl/pl = .44 to 1.24, gl/W = .31 to 1.06 (9 spp.).

MESOSOMA. (19) Pronotal lateral angle produced, forming rounded or sharp acute angle, or not produced, forming obtuse angle. Lateral ridge usually sharply angled, rarely rounded or carinate. Dorsal ridge carinate. (20) Mesoscutum not narrowed anteriorly, lip rounded. (22) Basal area of propodeum variously roughened, usually with weak plicae basally, smooth apically, or completely striate, rarely strongly so. (24, 25) Marginal cell of forewing usually narrowly truncate and appendiculate, as in *Pseudaugochloropsis* (Fig. 37), rarely acute; mc/wl = .61 to .66 (5 spp.). (30) Anterior basitarsal brush weakly defined.

METASOMA. (34) Sterna IV and often V with gradulus defined basally.

Male

HEAD. (35) Antenna moderately long, reaching scutellum, no plate areas. Flagellomere 2 usually slightly longer than 1, rarely 2 about 1.5 times 1, flagellomeres increase in length distally, sc/2 = 2.36 to 5.62, 2/1 = .68 to 1.48, 3/1 = 1.08 to 1.62, 10/1 = 1.24 to 2.11 (6 spp.). (36) Labrum with distal process well developed, triangular; basal elevation extending across basal area, weakly notched medially or entire.

METASOMA. (39) Tergum VII abruptly convex apically, post-gradular area sometimes somewhat indented and flattened; gradulus defined, sometimes weakly so, rarely absent. (40) Anal lip of proctiger without post-anal filaments*, usually with cuticular striations or markings. (41) Apical margin

of sternum III indented medially. (42) Sternum IV with distinctive median patches of setae, see subgeneric descriptions. (43) Sternum V with apex emarginate, rarely lobed lateral to emargination or medially; without distinctive clumps of setae. (44) Sternum VI weakly notched apically, median portion of postgradular area shiny, depressed, without setae, often with low longitudinal ridge. *Sterna V and VI frequently with narrow acrosternite, sternum VI frequently with small sclerotized median apodeme attached by membrane to acrosternite, homologous in position with spiculum**. (45) Sternum VII posteriorly slightly to strongly prolonged into rounded or truncate lobe, usually bearing short setae; apodemes recurved anteriorly. *Median well-sclerotized apodeme connected by membrane to sternum VII, extending anteriorly and overlapping spiculum*. Sternum VIII with posterior margin bearing no or few setae, see subgeneric descriptions; spiculum narrow; sternum VIII joining VII at apices of apodemes (Figs. 314-317).

(46) Gonobase (Figs. 397-402) with narrow ventral bridge, dorsal lobes slightly produced. (47) Ventral gonostylus a flattened seta-bearing lobe, continued anteriorly on inner edge of gonocoxite to level of volsella. Basal process of gonostylus absent. Dorsal gonostylus variable, see subgeneric descriptions. (48) Penis valve (Fig. 399) with ventral prong; rounded dorsal crest not sharply delineated from anterior dorsal surface of valve; inner flange variously developed medial to crest; lateral flange rarely developed. (49) Volsella (Fig. 400) with notch near apex, base more or less rounded or truncate; see subgeneric descriptions.

*Exceptions

Caenaugochlora costaricensis (Friese), a comparatively large species, is exceptional in having a gradually rounded preoccipital ridge. The type species of the subgenus *Ctenaugochlora, Caenaugochlora perpectinata* (Michener), is unique in having the pregradular areas of sterna V and VI (Figs. 258-259) greatly expanded, the antecosta being bowed anteriorly. *C. perpectinata* also has only a moderately long glossa, gl pl = .50, gl W = .32, with the salivary plate normal, not well defined, and bearing a V-shaped brace. An additional species of *Ctenaugochlora* has very short post-anal filaments on the proctiger, not pigmented or lined with microtrichia. A third species of this subgenus has the subapical tooth and outer posterior ridge of the mandibles of the female produced.

Species of *Caenaugochlora* are variously colored, and usually of moderate size and smaller than *Pseudaugochloropsis*, to which they are apparently most closely related. The quite different male genitalic and metasomal characters, as well as the more normal mouthparts, justify giving *Caenaugochlora* separate generic rank.

Subgenus **Caenaugochlora** Michener

Caenaugochlora (Caenaugochlora) Michener, 1954, Bull. Amer. Mus. Natur. Hist. 104:76. (Type species: *Caenaugochlora macswaini* Michener, 1954, original designation.)

Female

(9) *Compound eye usually bearing long hairs;* hairs rarely short, of normal size. (11) Basal elevation of labrum with proximal surface usually shiny, somewhat indented; rarely shallowly notched. (27) Hind tibial spur pectinate, as in *Pseudaugochloropsis* (Fig. 53). (29) Basitibial plate well defined, edges somewhat raised, narrowly rounded.

Male

(42) *Metasomal sternum IV* (Fig. 256) *bearing 1 or 2 distinctive pairs of setal clumps on raised tubercles, to either side of apical median depression.* Gradulus reaching antecosta medially, antecosta may be interrupted medially; postgradular area may bear specialized setae medially and at gradulus. (45) Posterior margin of sternum VIII (Fig. 314) strongly produced into a rounded, truncate, or slightly bilobed median projection. (47) Dorsal gonostylus (Fig. 398) a transparent thin or membranous longitudinal lobe bearing setae at its apex; lobe projecting from inner margin of dorsal ridge. Volsella emarginate medially, inner apical corner more or less produced.

Typical *Caenaugochlora* frequently resemble *Augochloropsis* in color pattern and size; they can easily be distinguished from the latter genus by the lack of metasomal vibrissae, the normal tegulae, basitibial plate, and epistomal sulcus. *Caenaugochlora costaricensis* (Friese) and its more northern close relatives or color varieties are about the size of *Pseudaugochloropsis graminea* (about 11 mm long) and resemble *Pseudaugochloropsis* closely in general appearance. The long hairs on the eyes of *C. costaricensis* and most smaller species of *Caenaugochlora* separate these bees from *Pseudaugochloropsis* and most other augochlorine genera, although they resemble in this respect *Caenohalictus* (not an augochlorine genus). Females of *Caenaugochlora* are also distinguished from *Pseudaugochloropsis* by the uniformly convex supraclypeal area, usually carinate or sharply angled preoccipital ridge, and usually weakly and obscurely punctured central area of the mesoscutum. Males can be separated externally from bees of most genera by the modifications of metasomal sternum IV; the antennae are not hooked. *Caenaugochlora* is a medium-sized but poorly collected genus, with species known from Mexico to Ecuador.

Michener (1954) proposed *Caenaugochlora* to replace *Caenohalictus* of authors other than Cameron, since the description by Cameron led Michener to believe that *Caenohalictus* was actually a senior synonym of *Rhinetula* Friese. However, an examination of the type species of *Caenohalictus* led Moure (1964) to restore *Caenohalictus* to its original meaning as separate

from *Rhinetula* (see Eickwort, 1967). Neither *Caenohalictus* nor *Rhinetula* are augochlorine genera. However, the series of bees upon which Michener (1954) based his description of *Caenaugochlora* are not *Caenohalictus*, but are actually related to *Pseudaugochloropsis*, as Michener realized.

Michener had proposed *Caenaugochlora s. l.* to include both *Caenaugochlora s. s.* and *Pseudaugochlora*, which he named to replace *Pseudaugochloropsis* as used by Moure (see discussion of *Pseudaugochloropsis*). Accepting Moure's concept of *Pseudaugochloropsis*, I earlier (Eickwort, 1967) tentatively synonymized *Caenaugochlora* with *Pseudaugochloropsis*, using the latter name as a replacement for *Caenaugochlora s. l.* in the sense of Michener (1954). Not having found species intermediate between the two groups, I now consider *Pseudaugochloropsis* and *Caenaugochlora* to be separate genera, although related.

Subgenus **Ctenaugochlora,** new subgenus

(Type species: *Neocorynura perpectinata* Michener, 1954.)

Female

(9) Compound eye with hairs normal, not long. (11) Basal elevation of labrum with surface flattened, roughened, strongly notched. (27) *Hind tibial spur* (Fig. 217) *closely pectinate, over 10 long teeth per spur.* (29) *Basitibial plate only defined posteriorly, obsolescent anteriorly.*

Male

(42) *Metasomal sternum IV* (Fig. 257) *with V-shaped patch of setae bordering slight median depression,* not otherwise modified. (45) Posterior margin of sternum VIII (Fig. 317) not produced; posterior margin of sternum VII broadly produced. (47) Dorsal gonostylus (Fig. 402) a small membranous extension without setae, extending from dorsal ridge which bears setae. (49) Volsella (Fig. 401) not notched on inner margin, inner apical corner not produced.

Caenaugochlora perpectinata is a black species with greenish tints, darkened anterior margins of the forewings, and strongly produced pronotal lateral angles. In general appearance it is strikingly similar to many species of *Neocorynura*, the genus in which it was first placed. The basitibial plate and tibial spur easily separate females of *Ctenaugochlora* from *Neocorynura* and *Caenaugochlora s. s.* Males can most easily be distinguished externally by the fourth metasomal sternum; the metasoma is somewhat elongate, as in *Caenaugochlora s. s.*, but not petiolate.

I have seen an additional green female *Ctenaugochlora* with orange legs and a long head; its mandibles have the subapical tooth and outer posterior ridge produced and the mouthparts are elongate, resembling those of *Caenaugochlora s. s.* In general appearance this specimen more closely resembles

Caenaugochlora s. s. than does *C. perpectinata*. The male of this species is unknown. Another species is known only by the male; the bees are reddish-violet and do not have the pregradular areas of metasomal sterna V and VI expanded in a manner similar to *C. perpectinata* (Figs. 258-259). The mesoscutum of known species of *Ctenaugochlora* is closely and distinctly punctate, unlike *Caenaugochlora s. s.* These three species are the only *Ctenaugochlora* known to me; they are from Costa Rica and Panama.

Derivation of *Ctenaugochlora:* Comb, plus *Augochlora*, in reference to the hind tibial spur of the female (feminine).

Genus **Megalopta** Smith

Megalopta Smith, 1853, Catalogue of hymenopterous insects in the collection of the British Museum 1:83. (Type species *Megalopta idalia* Smith, 1853, by designation of International Commission on Zoological Nomenclature, 1966, Opinion 788, Bull. Zool. Nomenclature 23:211.)

Megalopta (Megaloptella) Schrottky, 1906, Z. Syst. Hymenopter. Dipter. 6:312. (Type species: *Halictus ochrias* Vachal, 1904a, monobasic and original designation.)

Tmetocoelia Moure, 1943, Rev. Entomol. (Rio) 14:481. (Type species: *Megalopta sulciventris* Friese, 1926, original designation.)

Female

HEAD (Figs. 133-134). (1) Epistomal sulcus forming rounded acute angle, thus deeply lobed. Vertex swollen behind ocelli. (4) Preoccipital ridge gradually rounded. (5, 6) Hypostomal floor about 1.5 times as long as wide, l/w = 1.44, c/l = .82 (1 sp.). (7) Posterior flange projects slightly beyond occiput. (8) *Eyes enlarged, inner orbit slightly emarginate, eyes strongly convergent above, separated from lateral ocelli by less than ocellar diameter**; w/l = .082 to .092 (5 spp.). (10) *Ocelli enlarged**. (11) *Labrum* (Fig. 159) *with distal process expanded, as wide as basal area, margins flanged, labral fimbria short and on surface. Distal keel flat-topped basally. Basal area with lateral margins raised and rounded; basal tubercle medially indented.* (12) *Mandible* (Figs. 161-162) *with subapical tooth produced, supplementary teeth on inner surface.* (13) Distal portion of maxilla normal, relatively long and narrow, inner strip with narrow scale-like cuticular markings and abundant long setae on surface of strip. (14) Maxillary palpus, p/M = .31 to .35 (5 spp.). (15) Prementum relatively long and narrow, pl/W = .61 to .81 (4 spp.)*. (16) Salivary plate well sclerotized, similar to that of *Pseudaugochloropsis* (Fig. 27), brace not apparent. (17) Glossa very long, gl/pl = .77 to 1.05, gl/W = .44 to .62 (5 spp.). (18) Palpi normal, segments 2 plus 3 slightly longer than 1.

MESOSOMA. (19) *Pronotal dorsal ridge gradually rounded, very narrow. Anterior edge of lateral angle carinate; lateral ridge carinate and lateral surface striate* (Figs. 195-196). (20) Mesoscutal lip low and rounded. (22) Basal area of propodeum smooth or with weak striae. (24, 25) Marginal cell of fore-

wing long, mc wl = .62 to .68 (4 spp.). Apex of cell narrowly truncate. *Hamuli numerous, in single closely-spaced series**. (26) Hind tibia with short apical spine. (27) *Hind tibial spur pectinate, teeth slightly flattened and lamellate* (Fig. 220). (29) *Basitibial plate defined only posteriorly* (Fig. 205)*. (30) Anterior basitarsal brush well defined.

METASOMA. (31) Pseudopygidal area clothed with scale-like setae bordering median slit.

Male

HEAD. (35) Antenna moderately long, tip strongly beveled, flagellomere 2 1.25 to 1.5 times length of 1 but slightly shorter than 10, sc 2 = 2.20 to 2.89, 2 1 = 1.23 to 1.49, 3 1 = 1.49 to 1.72, 10/1 = 1.34 to 1.72 (4 spp.). (36) Labrum with triangular distal process, about as long as basal area, basal tubercle not notched and extending across base, similar to that of *Augochlora* (Fig. 154).

METASOMA. (39) Tergum VII abruptly angled apically, with long setae; gradulus absent. (40) Anal lip of proctiger with post-anal filaments, similar to those of *Pseudaugochloropsis* (Fig. 96), or filaments absent. (41) *Sternum III with apical margin bilobed medially, lobes with short strong setae* (Fig. 264), median depression present or absent. (42) *Sternum IV with apical margin notched laterally, bilobed medially; flap projecting medially just posterior to gradulus;* post-gradular area with patches of short setae or more uniformly clothed with long setae; antecosta meeting gradulus medially (Fig. 265). (43) Sternum V (Fig. 266) short and wide, notched medially with apical depression; gradulus broadly joining antecosta. (44) Sternum VI (Fig. 267) short and wide, deeply notched medially, slight longitudinal median ridge, antecosta sometimes absent medially. (45) Sternum VII projecting posterior to sternum VIII, posterior process bilobed and bearing setae, apodemes slightly recurved anteriorly. Sternum VIII with narrow spiculum; posterior median projection little developed, usually bearing setae medially; laterally joining sternum VII near apices of apodemes (Figs. 319-321).

(46) Gonobase (Figs. 403-404) with narrow ventral bridge, dorsal lobes slightly projecting over gonocoxites. (47) Ventral gonostylus a caudally directed lobe with seta-bearing flattened surface facing ventrally; setae also on dorsal surface of lobe. *Parapenial lobe well sclerotized, expanded apically, projecting to midline, ventral to penis valve.* Basal process of gonostylus absent. Dorsal gonostylus a long thin flap, sometimes bearing setae on ventral surface. (48) *Penis valve* (Fig. 405) *with large ventral prong and large, apparently eversible, dorsal crest apical to dorsal depression.* (49) Volsella (Fig. 406) with inner edge notched.

*EXCEPTIONS

The eyes and ocelli of one female specimen examined are not enlarged, but rather normal in size, comparable to those of other genera. This same

specimen has a relatively short prementum, pl/W = .42. It also has the hamuli somewhat clumped, and the basitibial plate defined apically and partially anteriorly, as well as posteriorly. According to Moure (1958b), *Megalopta ianthina* Smith and *M. nigrofemorata* Smith, described from the females, also have normal-sized ocelli.

Megalopta is a genus of large to very large bees; most species are nocturnal with enlarged eyes and ocelli. Most species are largely testaceous with abundant green reflections on the head and mesosoma, although one species examined lacks greenish reflections, those parts being brown instead. Representatives of the genus occur from Mexico to Argentina.

Excluding the small-eyed female cited as an exception above, the species available to me can be divided into two species groups. Specimens of one group have a weakly plicate basal area of the propodeum, post-anal filaments on the proctiger of the male, and also differ slightly from the second group in the exposed metasomal sterna and gonostyli of the male. Specimens of the second group have a completely smooth basal area of the propodeum, lack post-anal filaments, and the males bear unusual protuberances near the propodeal spiracles; these bumps are densely covered with short setae so as to appear felt-like. The differences between these groups do not merit subgeneric splitting at present; specimens not available to me may be intermediate or represent other species groups, judging from the descriptions quoted by Friese (1926).

Following its description by Smith (1853), who included two new species (*bituberculata* and *idalia*), *Megalopta* has almost universally been accorded generic status. Unfortunately, *M. bituberculata* Smith was designated as the type species (Cockerell, 1900). It was later discovered that *M. bituberculata* is actually a nomiine bee, belonging to *Reepenia* of the Indo-Australian region and probably mislabeled as coming from Brazil (Michener and Moure, 1964). Moure (1943) proposed the name *Tmetocoelia* for the species normally placed in *Megalopta,* excluding *M. bituberculata.* Later (1958b) he reviewed the nomenclatorial history of *Megalopta* and stated that *M. idalia* Smith should have been considered the type species, as the generic description referred primarily to that species. He named the genus *Megaloptodes* to accommodate *M. bituberculata.* Michener and Moure (1964) petitioned the International Commission on Zoological Nomenclature to use its plenary powers to designate *idalia* as the type species of *Megalopta,* and this request was granted (International Commission on Zoological Nomenclature, 1966). *Tmetocoelia* thereby became a synonym of *Megalopta,* and *Megaloptodes* of *Reepenia.*

Schrottky (1906) named *Megaloptella* as a subgenus of *Megalopta,* for *Megalopta ochrias* (Vachal). He later synonymized it with *Megalopta,* as did Moure (1958b).

Cockerell (1905b) published a key to Smith's species of *Megalopta*, noting that they did not constitute a natural group. Moure (1958b) redescribed Smith's species, leaving 4 species in *Megalopta* and placing the others in other genera.

Friese (1926) published an extensive revision and discussion of *Megalopta*, including the original descriptions of eight previously described species and descriptions of 14 new species. He doubtfully placed *Megaloptella* as a subgenus of *Megalopta*. He doubted the necessity of subdividing *Megalopta* but suggested that head structure and female tibial spur form should be considered in any attempt to do so (Friese included *Megaloptidia* as a synonym of *Megalopta*). He listed 40 species, not all currently placed in *Megalopta*.

Well known species of *Megalopta* include *M. genalis* Meade-Waldo from Central America, and *M. sodalis* (Vachal) and *M. amoena* (Spinola) (= *M. idalia* Smith, according to Sakagami and Moure, 1965) from South America.

Genus **Megommation** Moure

Female

HEAD. (1) Epistomal sulcus forming an approximately right angle. (2) *Clypeus and supraclypeal area strongly bowed outwards*, as in Fig. 129. *Clypeal teeth prominent*. (4) Preoccipital ridge rounded. (5, 6) Hypostomal floor long and narrow. (7) Posterior flange of hypostoma projects beyond occiput. (8) Inner orbit of compound eye moderately emarginate, w l = .114 to .128 (3 spp.). (10) Ocelli normal to enlarged, see subgeneric descriptions. (11) Labrum with distal process triangular, nearly as wide as basal area but shorter; basal elevation suborbicular, strongly protuberant, apical surface flattened, basal elevation as in labrum of *Pseudaugochloropsis* (Figs. 7-8). (12) *Mandible broad*, as in Fig. 166. (13) *Distal portion of maxilla long and very narrow, as in Ariphanarthra* (Fig. 182). Apex of galea pointed, no apical lobe. Inner strip with long setae on surface. (14) Maxillary palpus of normal length. (15) *Prementum very long and narrow, as in Ariphanarthra* (Fig. 171), pl W = .61, pw pl = .06 (1 sp.). (16) Salivary plate well defined, no V-shaped brace. (17) Glossa rather short, as in *Ariphanarthra*, gl l pl = .29, gl W = .18 (1 sp.). (18) Segments 2 plus 3 of labial palpus shorter than 1.

MESOSOMA. (19) Pronotal lateral angle not produced, obtuse. Dorsal ridge not carinate, weakly defined; lateral ridge rounded. (20) Mesoscutum not narrowed anteriorly, lip low and rounded. (22) *Basal area of propodeum smooth, without striae*. (24, 25) Marginal cell of forewing acute, mc l wl = .57 to .63 (3 spp.). (29) *Basitibial plate very short, little surpassing apex of femur*, well defined on all edges. (30) Anterior basitarsal brush apparently absent.

METASOMA. (32) Suprapygidial plate poorly defined, gradulus absent on tergum VI.

Male

HEAD. (35) Antenna reaching about to scutellum, plate areas present or absent; flagellomere 1 much longer than 2 and subequal to 10; sc/2 = 4.74 to 9.16, 2/1 = .53 to .66, 3/1 = .78 to .80, 10/1 = .97 to 1.17 (2 spp). (36) Labrum with basal area rather long, distal process not or scarcely formed, labrum less than 1.5 times wider than long. Basal elevation strongly protuberant, slightly notched medially or entire, extending across basal area.

METASOMA. (38) Metasoma oval, not elongate. (39) Tergum VII rather abruptly convex apically, no gradulus. (40) Anal lip of proctiger with postanal filaments. (41) Apical margin of sternum III produced and pointed medially. (42) *Sternum IV with row or rows of strong modified setae laterally on postgradular area, bordering gradulus;* gradulus interrupted medially, modified as in Figs. 262 and 263. (43) Sternum V weakly or strongly emarginate medially. (44) Sternum VI weakly notched apically, gradulus slightly notched medially. (45) Sternum VII produced posteriorly, bearing setae; apodemes recurved. Sternum VIII not produced posteriorly, few or no setae; laterally joining VII far from apices of apodemes. Spiculum moderately broad (Figs. 322-323).

(46) Gonobase (Figs. 407-410) with narrow ventral bridge, sharply angled dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus a large lobe broadly joining inner edge of gonocoxite, extending anteriorly to level of top of volsella, bearing setae. Basal process of gonostylus absent. Dorsal gonostylus a large partly membranous lobe, see subgeneric descriptions. (48) Penis valve with ventral prong and strong dorsal crest posterior to more or less well-defined dorsal depression; valve expanded medially and laterally. (49) Volsella indented medially and apically; shallow transverse ridge below notch; base prolonged laterally.

Megommation and its relatives, *Megaloptidia* and *Ariphanarthra,* are characterized by the strongly protuberant clypeus and supraclypeal area and very narrow mouthparts, distinctive without dissection. Species in these genera are rather shiny, weakly and obscurely punctured, with the basal area of the propodeum usually smooth. As a group they are poorly represented in collections.

A male of *Megaloptidia* was unfortunately not available to me for dissection; examination of its genitalic and sternal structures might lead to placing *Megommation* as a subgenus of it. At present I consider *Megommation* to consist of two well-separated subgenera.

Subgenus **Megommation** Moure

Megommation Moure, 1943, Rev. Entomol. (Rio) 14:479. (Type species: *Halictus insignis* Smith, 1853, monobasic and original designation.)

Female (Fig. 128)

(8)Eyes enlarged. (10) *Ocelli enlarged.* (27) *Hind tibial spur serrate, similar to outer spur.*

Male

(37) Inner hind tibial spur curved and rounded at tip. (40) Post-anal filaments of proctiger long. (42) Sternum IV with two pairs of rows of modified setae, extending nearly to posterior margin, posterior margin produced and truncate (Fig. 263). (43) Sternum V with deep rounded emargination posteriorly, gradulus bowed anteriorly and interrupted medially. (45) Sternum VII bilobed posteriorly (Fig. 323). (47) Ventral gonostylus with long stiff modified setae, as in Fig. 407. Small parapenial lobe present. Dorsal gonostylus (Fig. 408) consisting of broad membranous area bordering dorsal projection.

Megommation s. s. contains only the type species, *Megommation insigne* (Smith), a large (about 14 mm) brown species with enlarged ocelli. The ocelli and tibial spurs, as well as the larger size, distinguish *Megommation s. s.* from *Megaloptina*. *Megommation s. s.* is distinguished from *Megaloptidia* in the discussion of that genus. Specimens of *Megommation s. s.* are known from southern Brazil, Argentina, and Paraguay.

Moure (1943) gave other characteristics of *Megommation sensu stricto*.

Subgenus **Megaloptina,** new subgenus

(Type species: *Augochlora (Pseudaugochloropsis) ogilviei* Cockerell, 1930.)

Female (Fig. 129)

(8) Eyes normal. (10) *Ocelli normal or slightly enlarged.* (27) *Hind tibial spur pectinate* (Fig. 218), *teeth rather short.*

Male

(37) Inner hind tibial spur normal. *Dense patch of plumose setae on lateral surface of propodeum, just posterior to propodeal spiracle.* (40) Post-anal filaments very short and stubby. (42) Sternum IV with single short row of modified setae, not near posterior margin, which is unmodified or produced (Fig. 262). (43) Sternum V weakly emarginate apically, not modified. (45) Posterior margin of sternum VII produced medially, not bilobed (Fig. 322). (47) Ventral gonostylus with short setae, as in Fig. 409. Dorsal gonostylus complex (Fig. 410), an elongate partially membranous lobe projecting over ventral gonostylus, connected to medially projecting clear, thin flap.

Megaloptina is a poorly collected subgenus of medium sized, rather shiny, greenish bees abundantly suffused with brown. Unfortunately, the male of only one species was available to me for dissection, and the male genitalic and

sternal characters are based on this species alone. The tibial spur, more normal-sized eyes and ocelli, protuberant clypeus and supraclypeal area and the greatly narrowed mouthparts externally distinguish *Megaloptina* from any genus with which it could be confused. The clypeus of the male is strongly beveled, similar to that of *Ariphanarthra* but without a dividing carina.

I have seen specimens of five species of *Megaloptina,* but have been able to associate a name with only one species, *Megommation (Megaloptina) ogilviei* (Cockerell) new combination. Judging by the descriptions given by Smith (1879) and Cockerell (1905a), the male of *Augochlora festivaga* Dalla Torre (= *A. festiva* Smith, 1879) from Brazil belongs to *Megommation s. l.* and probably to *Megaloptina.* This species bears unusual tufts of pubescence on the propodeum as does the species I have examined, is medium sized and green but has "gigantic ocelli" (Cockerell, 1905a) and the middle of the apical margin of metasomal sternum IV is produced. Cockerell (1905a, 1930) recognized the unusual nature of *M. festivaga* and *ogilviei* but did not propose separate generic status for them, placing them in *Augochlora.* Species of *Megaloptina* are known from Costa Rica, Colombia, Guyana, Bolivia and Brazil.

Derivation of *Megaloptina:* Diminutive of *Megalopta* (feminine).

Genus **Megaloptidia** Cockerell

Megalopta (Megaloptidia) Cockerell, 1900, Proc. Acad. Natur. Sci. Philadelphia 52:373. (Type species: *Megalopta (Megaloptidia) contradicta* Cockerell, 1900, monobasic and original designation.)

Female

HEAD (Fig. 130). (1) Epistomal sulcus forming an approximately right angle. (2) *Clypeus and supraclypeal area strongly bowed outwards, as in Megommation* (Fig. 129). *Clypeal teeth broad.* (4) Preoccipital ridge rounded. (5, 6) Hypostomal floor long and narrow. (8) Inner orbit of compound eye strongly emarginate, w/l = .148 (1 sp.); *eyes greatly enlarged, projecting above vertex and nearly reaching lateral ocelli and subantennal sulci.* (10) *Ocelli enlarged.* (11) Labrum with distal process triangular, shorter than basal area, basal elevation suborbicular, strongly protuberant, apical face flattened, as in *Megommation.* (12) *Mandible broad, outer posterior ridge produced, as in Ariphanarthra* (Fig. 167). (13) *Distal portion of maxilla long and very narrow, as in Ariphanarthra* (Fig. 182). Apex of galea pointed, no apical lobe. Inner strip with long setae on surface. (14) Maxillary palpus long and slender, apical segments slightly flattened, p/M = .31 (1 sp.). (15) *Prementum very long and narrow, as in Ariphanarthra* (Fig. 171), pl/W = .68, pw/pl = .06 (1 sp.). (16) Salivary plate well defined, no V-shaped brace. (17) Glossa rather short, as in *Ariphanarthra,* gl/pl = .25, gl/W = .17 (1 sp.). (18) Segments 2 plus 3 of labial palpus shorter than 1.

MESOSOMA. (19) Pronotal lateral angle not produced, obtuse. Dorsal ridge not carinate, weakly defined; lateral ridge rounded. (20) Mesoscutum not narrowed anteriorly, lip low and rounded. (22) *Basal area of propodeum smooth, without striae.* (24, 25) *Marginal cell of forewing narrowly truncate and appendiculate, marginal cell long,* mc / wl = .74 (1 sp.). (27) Hind tibial spur serrate. (29) Basitibial plate not short, much surpassing apex of femur, well defined on all edges, narrowly rounded. (30) Anterior basitarsal brush weakly formed.

Male

HEAD. (35) Antenna with flagellomere 1 longer than 2, apical flagellomeres not examined, sc / 2 = 5.50, 2 / 1 = .77 (1 sp.). (36) Labrum with basal area rather long, strongly arched, distal process not or scarcely formed, as in *Megommation*. Basal elevation strongly protuberant, not notched, extending across basal area.

METASOMA. (42) *Sternum IV with posterior margin bilobed, profound median notch, resulting lobes strongly pilose.*[1] (43) Sternum V normal.[1] (44) Sternum VI weakly notched apically.[1]

Megaloptidia contains only the type species, *M. contradicta* (Cockerell). Through the courtesy of Dr. Jerome Rozen, Jr., of the American Museum of Natural History, I have been able to examine a series of females of *Megaloptidia*. This rather large (about 12 mm) species, probably *M. contradicta*, is largely ferruginous brown with slight metallic tints and most closely resembles *Megommation insigne*, from which it can be easily distinguished by the huge eyes projecting above the vertex and by the basitibial plate, and by the bilobed fourth metasomal sternum of the male. The narrow mouthparts will distinguish *Megaloptidia* from any other genera, such as *Megalopta*, with which it could be confused. In lateral view, the head of *Megaloptidia* is quite striking, as it is very narrow, the genae being much narrower than the eyes.

Unfortunately, the only male available to me is lacking the distal portions of the antennae and metasoma. It was borrowed from the Academy of Natural Sciences in Philadelphia and was collected in Santarem, Brazil, and probably formed part of Cockerell's type series. *Megaloptidia* is very similar to *Megommation* and *Ariphanarthra* but their exact relationship cannot be determined until the male terminalia can be studied. *Megaloptidia* is known only from Brazil.

The original subgeneric description of *Megaloptidia* by Cockerell (1900) was very sketchy, describing principally the wing venation. Moure (1958b) described the genus in much greater detail, differentiating it from *Megommation*.

[1] Not examined; as described by Moure (1958b).

Genus **Ariphanarthra** Moure

Ariphanarthra Moure, 1951, Dusenia 2:137. (Type species: *Ariphanarthra palpalis* Moure, 1951, monobasic and original designation.)

Female

HEAD (Figs. 131-132). (1) Epistomal sulcus forming right angle. (2) *Clypeus and supraclypeal area strongly bowed outwards,* as in Fig. 132. Face deeply impressed above supraclypeal area. (4) Preoccipital ridge rounded. (5) Hypostomal floor long and narrow, l/w = 1.89 (1 sp.). (6) Hypostomal bridge broadly joins posterior margin of hypostoma. (8) Inner orbit of compound eye moderately emarginate, w/l = .125 (1 sp.), eyes slightly enlarged. (10) Ocelli slightly enlarged. (11) Labrum with distal process triangular, as wide as basal area but shorter; basal elevation suborbicular, strongly protuberant, apical face flattened, as in *Megommation.* (12) *Mandible broad, outer posterior ridge produced* (Fig. 167). (13) *Distal portion of maxilla long and very narrow* (Fig. 182). Apex of galea pointed, no apical lobe. Inner strip with long setae on surface. (14) *Maxillary palpus extraordinarily long, reaching to metasoma at rest, segments 3-6 greatly lengthened and flattened, segments 1 and 2 much shorter and rounded,* as in Fig. 182. (15) *Prementum very long and narrow, higher than wide apically* (Fig. 171), pl/W = .88, pw/pl = .05 (1 sp.). (16) Salivary plate well defined, no V-shaped brace. (17) Glossa rather short, gl/pl = .21, gl/W = .19 (1 sp.). (18) Segments 2 plus 3 of labial palpus shorter than 1.

MESOSOMA. (19) Pronotal lateral angle not produced, obtuse. Dorsal ridge carinate; lateral ridge rounded. (20) Mesoscutum not narrowed anteriorly, lip rounded. (22) Basal area of propodeum weakly striate basally, smooth apically. (24, 25) Marginal cell of forewing acute, rather long, mc/wl = .66 (1 sp.). (27) *Hind tibial spur with long serrations* (Fig. 219). (29) Basitibial plate of normal length, well defined on all edges, pointed. (30) Anterior basitarsal brush well-defined.

Male

HEAD. (35) Antenna reaching about to scutellum, no plate areas, flagellomere 1 longer than 2 but shorter than 10; sc/2 = 4.34, 2/1 = .82, 3/1 = 1.01, 10/1 = 1.31 (1 sp.). Clypeus with distal portion abruptly declivous, set off from apical portion by carina. (36) Labrum with basal elevation strongly protuberant, not extending across basal area, not notched; distal process not examined.

METASOMA. (38) Metasoma oval, not elongate. (39) Tergum VII strongly depressed beneath apodemes (Fig. 228), abruptly convex apically, no gradulus, long setae in single row near posterior margin. (40) Anal lip of proctiger with long post-anal filaments. (42) *Sternum IV unmodified,* with very short setae except laterally, dense medially. (43) Sternum V with postgradular area densely clothed with rather short setae, longer near posterior margin, posterior

margin slightly emarginate medially. (44) Sternum VI with setae as on V, posterior margin rather strongly notched medially. (45) Sternum VII not produced posteriorly, bearing setae, apodemes moderately recurved. Sternum VIII not produced posteriorly, without setae; laterally joining VII far from apices of apodemes. Spiculum moderately narrow (Fig. 324).

(46) Gonobase (Figs. 411-412) with narrow ventral bridge, rounded dorsal lobes strongly projecting over gonocoxites. (47) Ventral gonostylus an apically-projecting lobe bearing long setae on its ventral surface, setae longest apically. Basal process of gonostylus absent; parapenial lobe a narrow thin flap. Dorsal gonostylus a large membranous swollen process, surpassing ventral gonostylus, variously expanded in cleared specimens (inflatable?). (48) Penis valve with ventral prong and low longitudinal dorsal ridge merging anteriorly into slight dorsal depression. Valve expanded medially and laterally. (49) Volsella indented medially, inner apical angle projecting ventrally; transverse ridge below notch; base truncate.

Ariphanarthra contains only the type species *A. palpalis* Moure, a large (about 9 mm) bright bluish, rather shiny species. It is noteworthy for the extraordinary development of the maxillary palpi of both sexes, which trail beneath the bee and provide the best recognition character for the genus. The unusual shape of the head is also distinctive, as illustrated in Fig. 132. In most characters, *Ariphanarthra* resembles *Megaloptidia* and its relatives. The genus is known from southern Brazil and Paraguay.

Moure (1951) has provided a detailed description of the genus and type species.

Genus **Chlerogella** Michener

Chlerogella Michener, 1954, Bull. Amer. Mus. Natur. Hist. 104:75. (Type species: *Chlerogella elongaticeps* Michener, 1954, monobasic and original designation.)

Female

HEAD (Fig. 135). (1) *Epistomal sulcus forming acute angle, epistomal lobe protruding into clypeus.* (3) *Malar area greatly elongate, nearly twice as long as distance between mandibular articulations, head thereby very elongate.* (4) Preoccipital ridge rounded. (5) Hypostomal floor longer than wide, not measured. (8) Inner orbit of compound eye weakly emarginate, w l = .088 (1 sp.). (11) Basal elevation of labrum low, elongate, rounded; basal area raised to either side of central elevation. Distal process not examined. (13-17) Mouthparts not dissected, not greatly narrowed or obviously modified, maxillary palpi rather long and slender.

MESOSOMA. (19) *Pronotum* (Fig. 198) *convex dorsally, lateral angle and lateral ridge completely absent, dorsal ridge rounded.* (20) *Mesoscutum joining pronotum almost at same level, mesoscutal lip almost absent.* (22) Basal area of propodeum longer than scutellum, smooth, no plicae. (24, 25) Mar-

ginal cell of forewing acute, very long, mc/wl = .70 (1 sp.). (27) Hind tibial spur pectinate, teeth long and pointed. (29) Basitibial plate defined on all edges, narrowly rounded. (30) Anterior basitarsal brush weakly defined.

Chlerogella is known only from the very unusual type species. *C. elongaticeps* Michener; this is a medium-sized (7.5 mm) lightly punctured mostly testaceous species with green tints. The highly elongate head and malar areas set *Chlerogella* apart from all other augochlorine genera except *Chlerogas,* whose species are larger and have more normal pronotal structure, and a bituberculate scutellum. Some species of *Caenohalictus,* a non-augochlorine genus, also have long heads with elongate malar areas; these species are easily distinguishable by the dense long hairs on their eyes and normal pronotal structure. The male of *Chlerogella* is unfortunately unknown. I have seen only the holotype specimen of *C. elongaticeps,* from Panama.

Michener (1954) presented additional generic and specific characters and illustrated the head of *C. elongaticeps.*

Genus **Temnosoma** Smith

Temnosoma Smith, 1853, Catalogue of hymenopterous insects in the collection of the British Museum 1:38. (Type species: *Temnosoma metallicum* Smith, 1853, monobasic.)

Micraugochlora Schrottky, 1909, Rev. Mus. La Plata 16:138. (Type species: *Micraugochlora sphaerocephala* Schrottky, 1909a, monobasic.) NEW SYNONYMY.

Temnosoma (Temnosomula) Ogloblin, 1953, Bol. Soc. Entomol. Argentina 2:2. (Type species: *Temnosoma (Temnosomula) platensis* Ogloblin, 1953, monobasic and original designation.) NEW SYNONYMY.

Female

HEAD (Fig. 138). (1) Epistomal sulcus forming obtuse angle. (2) Clypeus entirely green, coarsely punctate. (4) Preoccipital ridge sharply angled dorsally. Vertex produced above ocelli. (5, 6) Hypostoma about 1.5 times longer than wide, l/w = 1.50 to 1.58, c/l = .81 to .82 (2 spp.). (7) Posterior flange projects beyond occiput. (8) Inner orbit of compound eye moderately emarginate, w/l = .117 to .125 (2 spp.). (11) *Labrum* (Fig. 160) *with distal process expanded and truncate apically, distal process merging gradually into basal area, no distal keel.* Labral fimbria on anterior surface of distal process. Basal elevation notched medially; basal area swollen lateral to elevation. (12) *Mandible* (Fig. 168) *lacking subapical tooth, resembling mandible of male.* (13) Distal portion of maxilla rather short and broad, normal, inner strip with broad scale-like cuticular markings and without long setae, except apically. (14) Maxillary palpus, p/M = .28 to .36 (3 spp.). (15) *Prementum* (Fig. 172) *with anterior surface transparent, thin, premental thickenings defined only apically,* pl/W = .59 to .65, pw/pl = .17 to .18 (3 spp.). (16) Salivary plate (Fig. 174) normal, V-shaped brace. (17) Glossa short, gl/pl = .23 to .32, gl/W = .14 to .20 (3 spp.).

MESOSOMA. (19, 20) *Pronotum laterally not concave, mesoscutal lip almost absent.* Lateral angle (Fig. 197) rounded, not at all produced; lateral ridge

short and rounded. Dorsal ridge carinate. Ridge present on lateral surface of pronotum, running below lateral ridge from anterior surface to join anterior margin of pronotum below pronotal lobe. (21) Tegula (Fig. 200) entirely green, coarsely punctate. (22) Basal area of propodeum pitted basally, distally smooth with transverse striae. (23) Lateral carinae absent, posterior face coarsely punctate. (24, 25) Marginal cell of forewing acute, mc/wl = .63 to .65 (2 spp.). Second submarginal cell narrow or absent. (27) *Hind tibial spur* (Fig. 221) *serrate, similar to outer spur.* (28-30) *Scopa, mesofemoral brush, penicillus, basitibial plate, and anterior basitarsal brush all absent; legs resemble those of male.*

METASOMA. *Terga I-III very coarsely punctate, postgradular areas just posterior to gradulus strongly depressed, often with coarse transverse striae.* (31) *Pseudopygidial area of tergum V lacking, posterior marginal area as in male.* (32) Tergum VI (Fig. 229) narrow apically, pygidial plate narrowly rounded, suprapygidial plate poorly defined, gradulus absent. (34) Sterna IV and V resemble those of male (without basal post-gradular zone of long setae), not resembling normal female sterna. Sternum VI narrow apically, gradulus strong.

Male

HEAD. (35) Antenna short, pedicel and scape as in Fig. 180, no plate areas; sc 2 = 2.74 to 2.98, 2/1 = 1.64 to 1.78, 3/1 = 1.67 to 1.83, 10/1 = 1.64 to 1.95 (3 spp.). (36) *Labrum as in female* (Fig. 160), basal elevation extending across basal area.

METASOMA. (39) Tergum VII (Figs. 230-231) prolonged apically, gradually convex, apical margin bilobed, gradulus absent. (40) Anal lip of proctiger (Fig. 232) without post-anal filaments. (42-44) Sterna IV to VI (Figs. 260-261) with apodemes small, zone of dense long simple setae at base of post-gradular areas of sterna V and VI. Sternum VI weakly notched, postgradular area without setae centrally, shiny. (45) *Sternum VII with only apodemes sclerotized, centrally represented by seta-bearing membrane.* Posterior margin of sternum VIII more or less produced medially, usually bearing setae; laterally joining VII at apices of apodemes. Spiculum narrow (Fig. 318).

(46) Gonobase (Figs. 413-416) rather small, with rather wide ventral bridge and small dorsal lobes. (47) Ventral gonostylus a very large lobe, bearing setae on its ventral surface, with very long setae on its dorsal margins. Small membranous parapenial lobe present basal to or beneath ventral gonostylus; basal process of gonostylus absent. Dorsal gonostylus a simple seta-bearing ridge behind ventral gonostylus. (48) *Penis valve* (Fig. 416) *with greatly prolonged dorsal prong arising basal to dorsal depression and extending apically to surpass dorsal crest;* ventral prong absent. (49) Volsella (Fig. 415) very small, rounded or tapered basally.

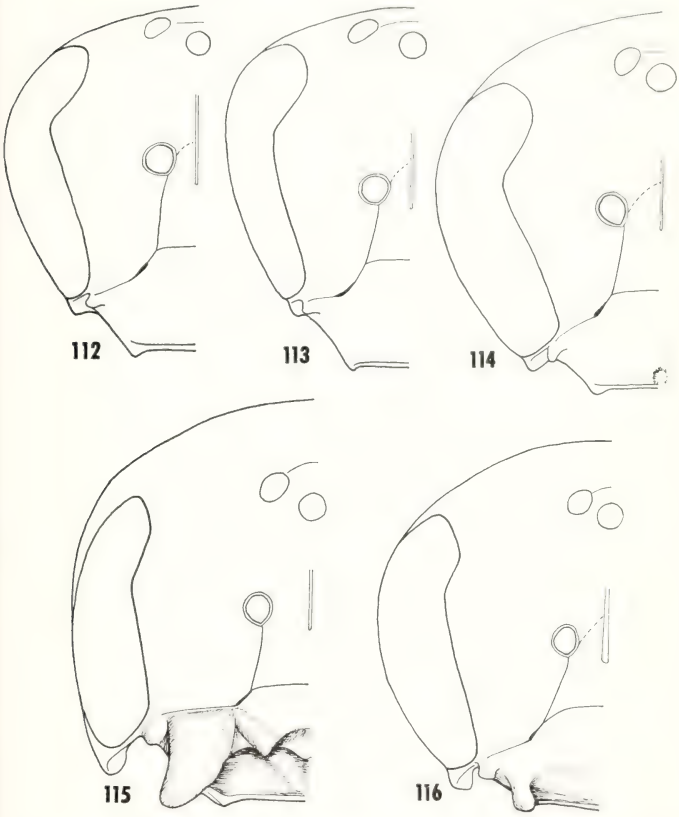
Species of *Temnosoma* are among the most distinctive halictine bees, resembling chrysidid wasps more than bees in general appearance. The small (less than ten species) closely knit genus is characterized by extremely coarse punctation, bright green or blue coloration and lack of all pollen-collecting apparatus in the female. Males and females resemble each other so closely that separation of sexes is difficult without a microscope; the last externally visible metasomal terga and sterna offer the best sexual characters. Species range in size from small to medium, and are found from Arizona to Argentina.

Smith's (1853) original description of *Temnosoma* gave no inkling of the unusual characteristics of this genus, as he stressed the mouthparts and wing venation, but his description of the type species pointed out the punctation and metasomal characters. *Temnosoma* has been correctly recognized by all authors to date. Due to the lack of scopa, most early authors considered it closely related to *Sphecodes,* and Ducke (1912) placed *Temnosoma* as a subgenus of *Sphecodes.* In actuality, *Sphecodes* and *Temnosoma* are not closely related, their concurrent characters being apparently convergent, due to a presumed social parasitic existence. Friese (1924) revised *Temnosoma,* recognizing six species.

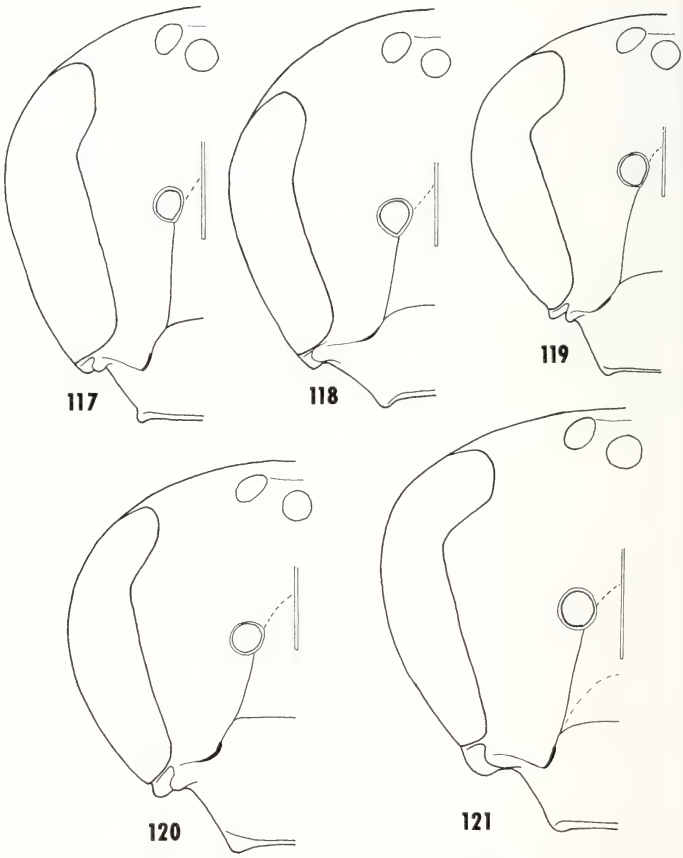
Schrottky (1909a) erected *Micraugochlora* for a small coarsely punctate green bee with simple tibial spurs. He placed *Micraugochlora* in the Panurgidae due to its two submarginal cells and compared it with *Gastrohalictus* (= *Dialictus,* a subgenus of *Lasioglossum*). His description gave little hint of its similarity to *Temnosoma.*

Ogloblin (1953, 1954) described the subgenus *Temnosomula* for a new species with two submarginal cells. Ogloblin (1954) accurately described and illustrated the hidden male sterna and genitalia of his species. Moure has examined the types of both *Temnosomula* and *Micraugochlora* and determined that *Micraugochlora sphaerocephala* Schrottky, 1909a, is a senior synonym of *Temnosoma platensis* Ogloblin, 1953, and the synonymy should be credited to him. Through Padre Moure's courtesy, I have been able to examine a paratype of *Temnosoma platensis.* I consider this species to be not subgenerically distinct; the differences in the hidden sterna that Ogloblin described are minor.

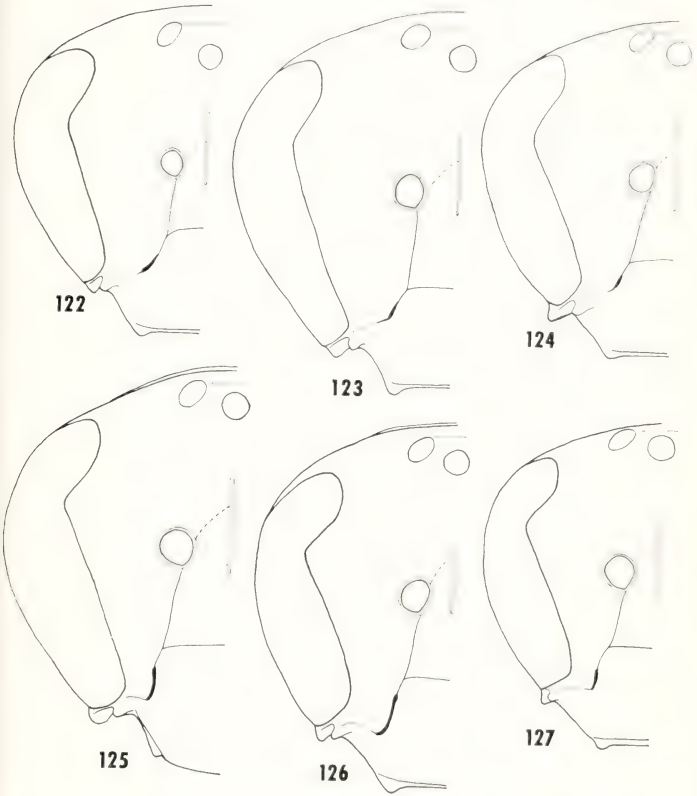
The best known species of *Temnosoma* are *T. smaragdinum* Smith from the Southwestern United States (Timberlake, 1958), Mexico, and Central America, and *T. metallicum* Smith from South America.



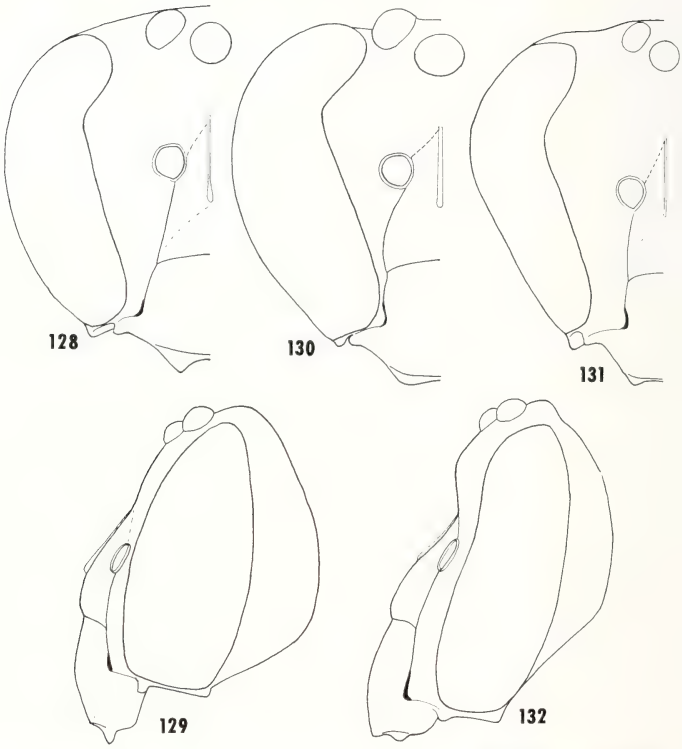
Figs. 112-116. Heads of female Augochlorini. 112, *Corynura* (*Corynura*) *chilensis* (Spinola); 113, *Halictillus* sp.; 114, *Rhinocorynura brisei* (Smith); 115, *Rhinocorynura inflaticeps* (Ducke); 116, *Rhinocorynura* sp.



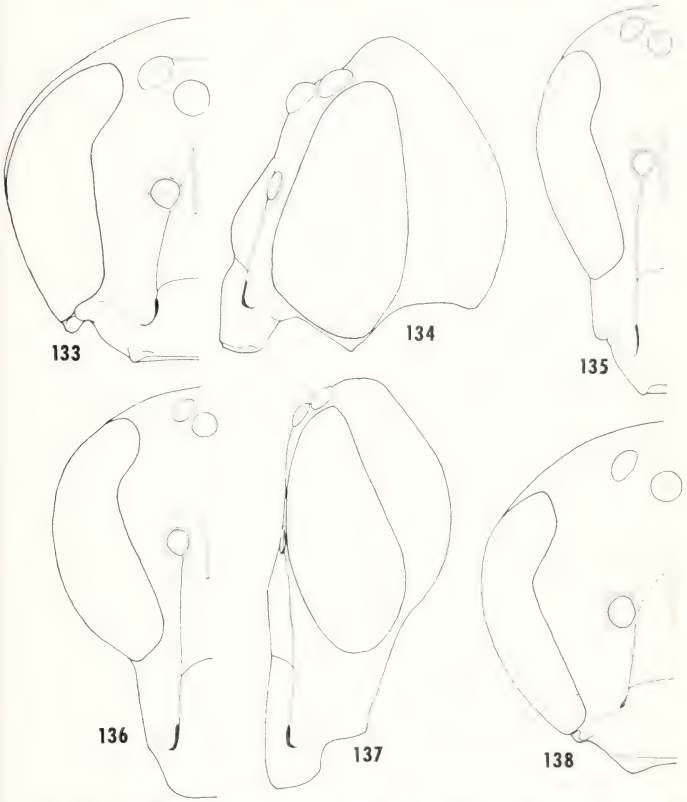
FIGS. **117-121.** Heads of female Augochlorini. **117,** *Corynurella mourei* n. sp.; **118,** *Rhectomia pumilla* Moure; **119,** *Neocorynura (Neocorynura) pubescens* (Friese); **120,** *Paroxystoglossa transversa* Moure; **121,** *Andinaugochlora micheneri* n. sp.



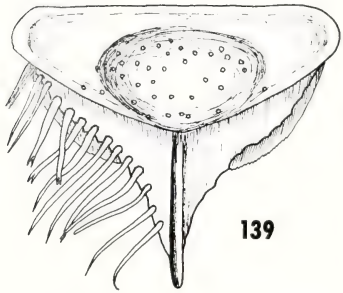
Figs. 122-127. Heads of female Augochlorini. 122, *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius); 123, *Thectochlora alaris* (Vachal); 124, *Ceratalictus theia* (Schrottky); 125, *Augochlora* (*Mycterochlora*) *repandirostris* (Vachal); 126, *Augochlora* (*Augochlora*) *pura* (Say); 127, *Augochlorella striata* (Provancher).

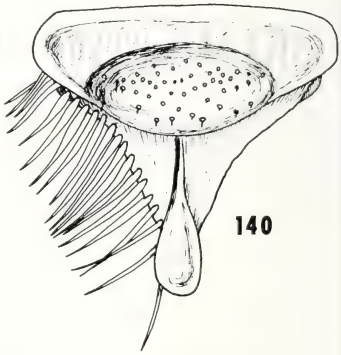


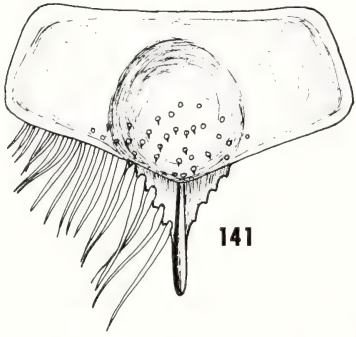
FIGS. **128-132.** Heads of female Augochlorini. **128,** *Megommation (Megommation) insigne* (Smith); **129,** *Megommation (Megaloptina)* sp.; **130,** *Megaloptidia ?contradicta* (Cockerell); **131-132,** *Ariphanarthra palpalis* Moure.

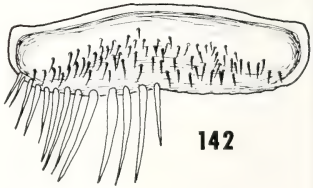


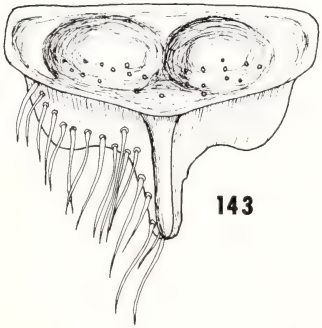
Figs. 133-138. Heads of Augochlorini. 133-135, 138, females: 136-137, male. 133-134, *Megalopta genalis* Meade-Waldo: 135, *Chlerogella elongaticeps* Michener: 136-137, *Chlerogas hirsutipennis* Cockerell; 138, *Temnosoma smaragdinum* Smith.

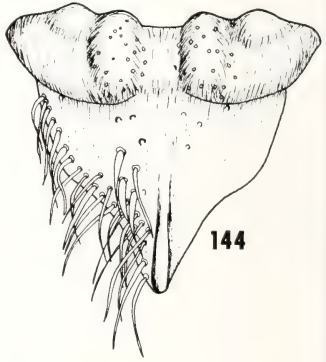




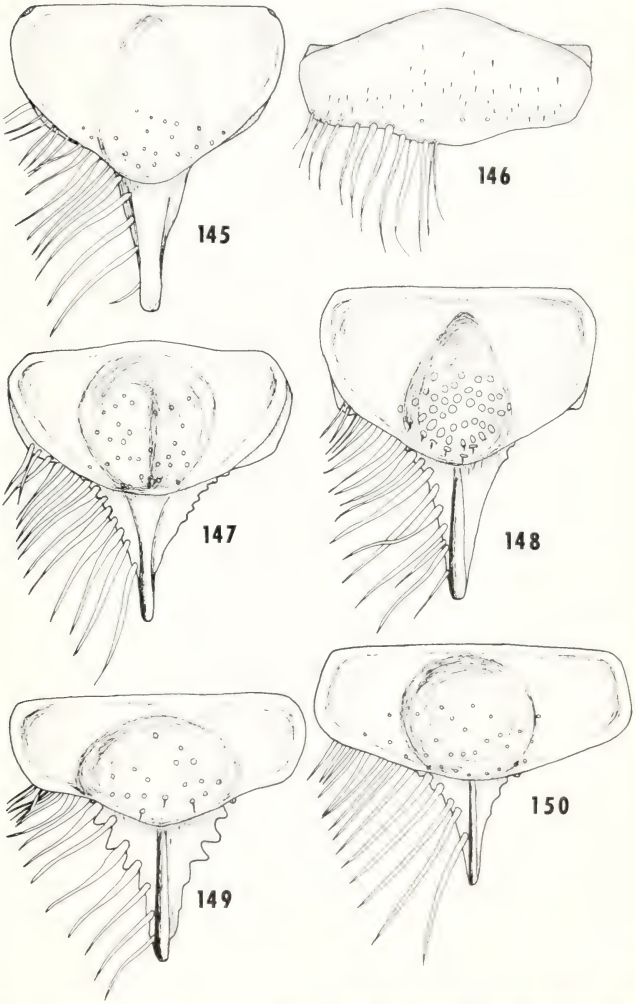




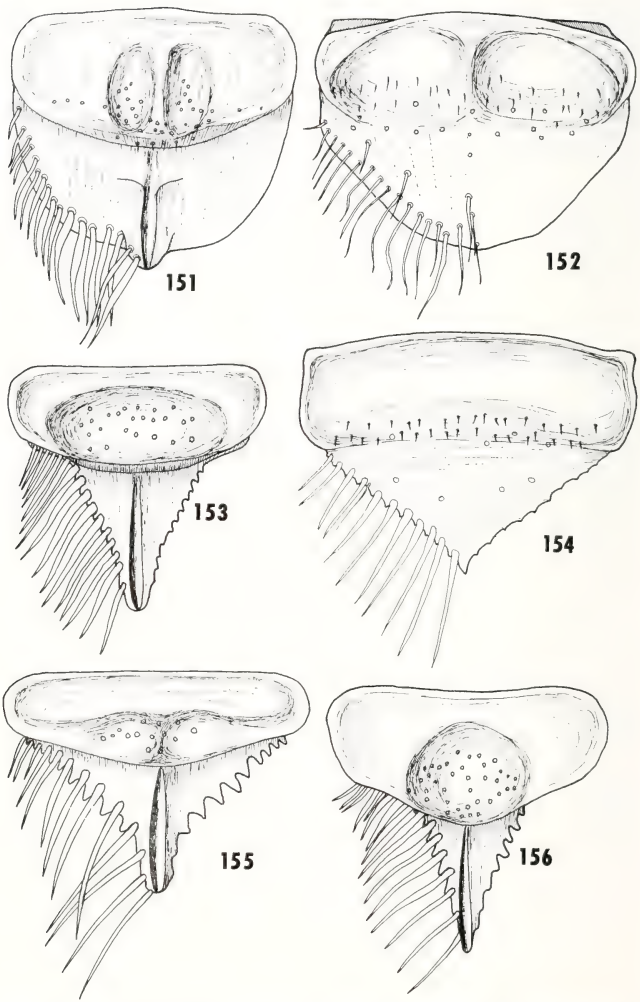




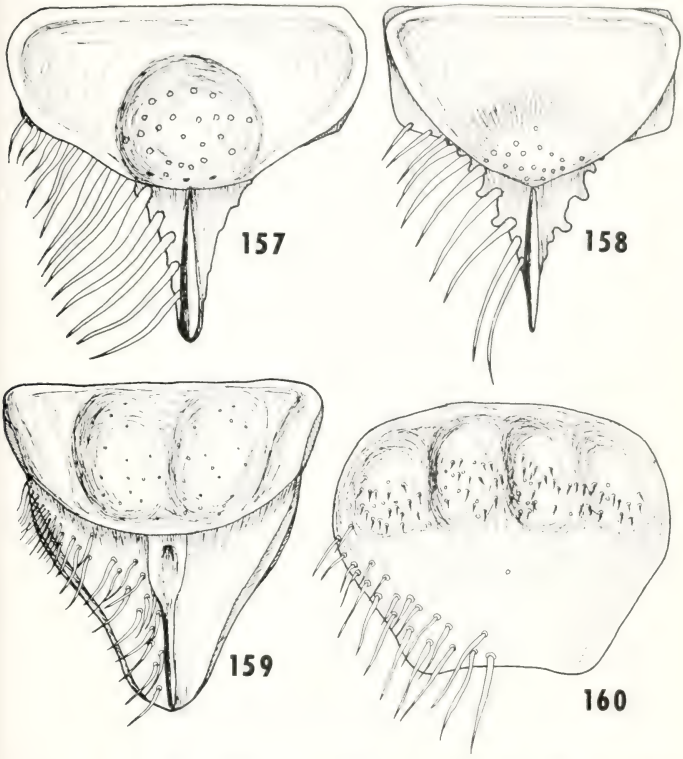
FIGS. **139-144.** Labra of Augochlorini. **139-141, 143-144,** females; **142,** male. **139,** *Corynura (Corynura) chilensis* (Spinola); **140,** *Corynura (Callochlora) chloris* (Spinola); **141,** *Halictillus* sp.; **142,** *Corynura (Corynura) chilensis* (Spinola); **143,** *Rhinocorynura briseis* (Smith); **144,** *Rhinocorynura* sp.



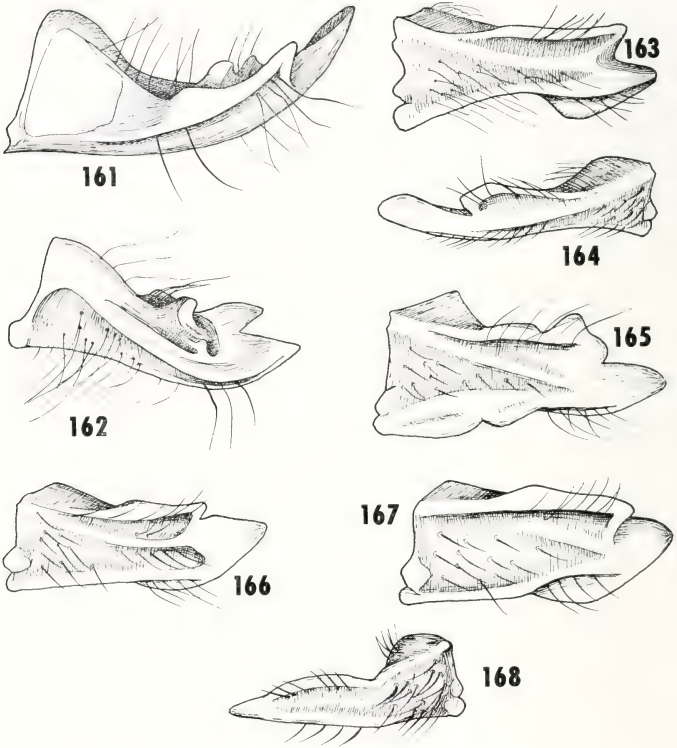
Figs. 145-150. Labra of Augochlorini. 145, 147-150, females; 146, male. 145-146, *Neocorynura (Neocorynura) pubescens* (Friese); 147, *Pereustoglossa transversa* Moure; 148, *Andinaugochlora micheneri* n. sp.; 149, *Thectochlora alata* (Vachal); 150, *Augochlorodes turrifaciens* Moure.



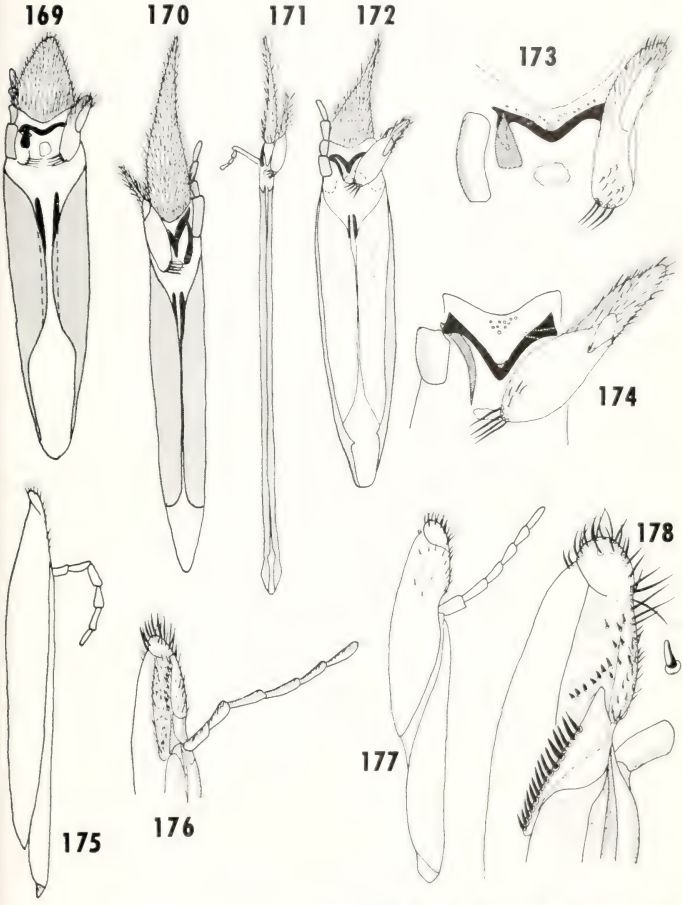
FIGS. **151-156.** Labra of Augochlorini. **151-152,** *Augochloropsis (Paraugochloropsis) metallica* (Fabricius) (151, female; 152, male); **153-154,** *Augochlora (Augochlora) pura* (Say) (153, female; 154, male); **155,** *Augochlora (Mycterochlora) repandirostris* (Vachal) female; **156,** *Augochlora (Oxystoglossella) antonita* Michener female.



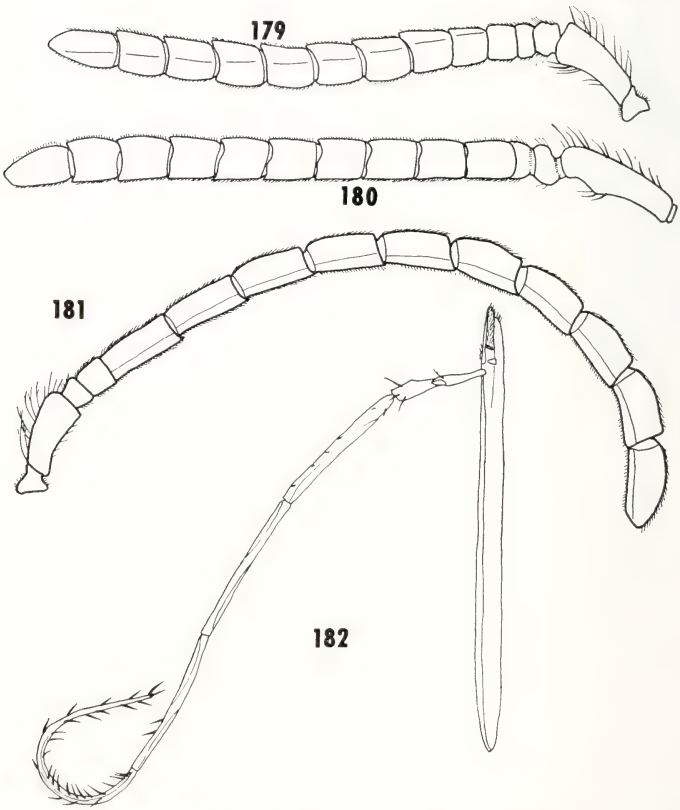
Figs. **157-160.** Labra of female Augochlorini. **157,** *Augochloropsella striata* (Provancher); **158,** *Pereirapis* sp.; **159,** *Megalopta genalis* Meade-Waldo; **160,** *Temnosoma smaragdinum* Smith.



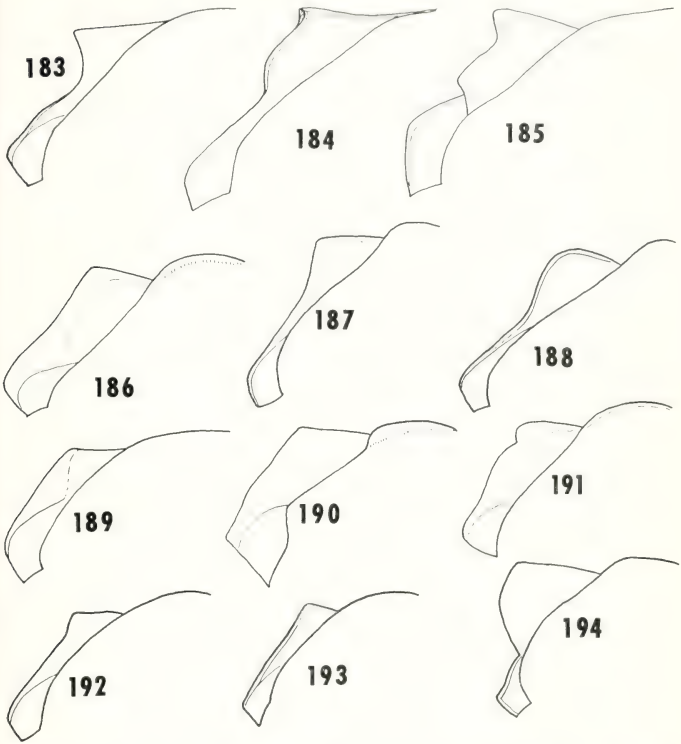
FIGS. **161-168.** Mandibles of female Augochlorini. **161-162,** *Megalopta genalis* Meade-Waldo (161, anterior view; 162, inner view);**163-168,** outer views. **163,** *Augochlora (Augochlora) pura* (Say); **164,** *Augochlora (Oxystoglossella)* sp.; **165,** *Rhinocorynura* sp.; **166,** *Megommation (Megommation) insigne* (Smith); **167,** *Ariphanarthra palpalis* Moure; **168,** *Temnosoma smaragdinum* Smith.



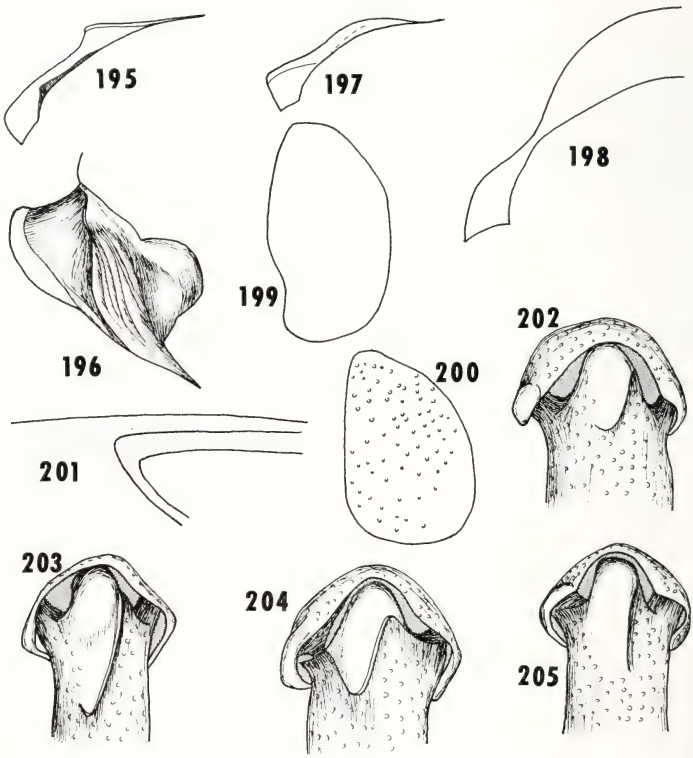
Figs. 169-178. Mouthparts of Augochlorini. 169-172, distal portions of labia, anterior views. 169, *Corynura (Corynura) chilensis* (Spinola); 170, *Augochlora (Augochlora) pura* (Say); 171, *Ariphanarthra palpalis* Moure; 172, *Temnosoma smaragdinum* Smith. 173-174, bases of ligulae, anterior views. 173, *Corynura (Corynura) chilensis* (Spinola); 174, *Temnosoma smaragdinum* Smith. 175-178, distal portions of maxillae. 175-176, *Augochlora (Augochlora) pura* (Say) (175, posterior view; 176, post-palpal portion, anterior view); 177-178, *Corynura (Corynura) chilensis* (Spinola) (177, posterior view; 178, post-palpal portion, anterior view).



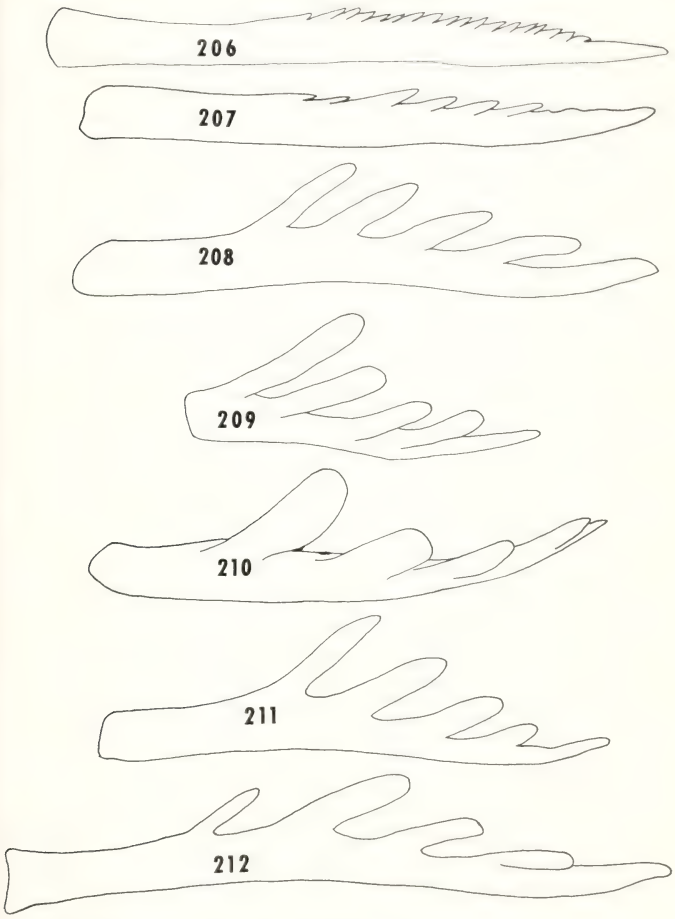
FIGS. **179-182.** Head appendages of Augochlorini. **179-181,** antennae of males. **179,** *Augochlora (Augochlora) pura* (Say); **180,** *Temnosoma smaragdinum* Smith; **181,** *Corynura (Corynura) chilensis* (Spinola). **182,** distal portion of maxilla of *Ariphanarthra palpalis* Moure, anterior view.



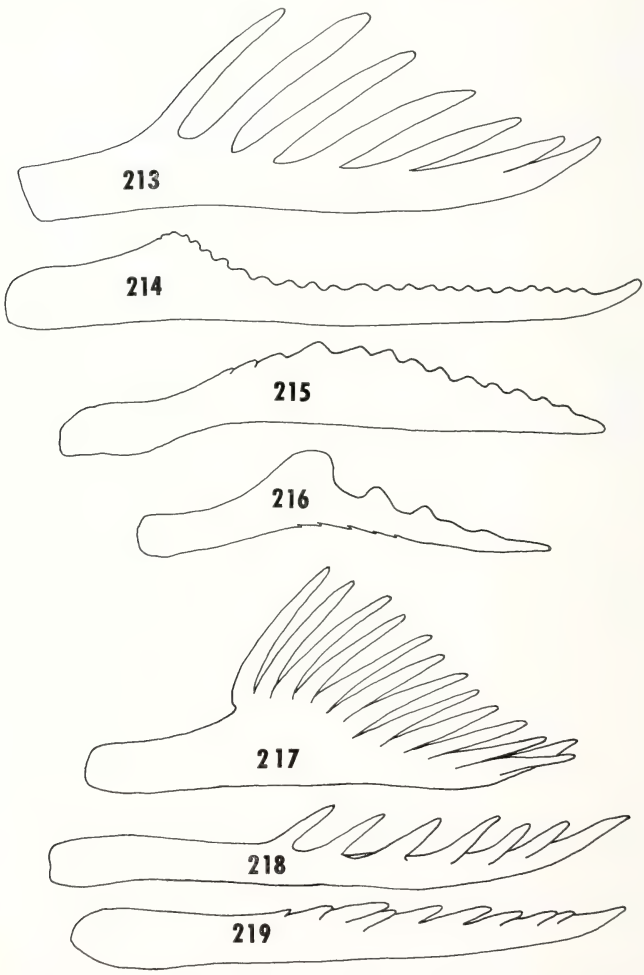
Figs. 183-194. Pronota and mesoscutal lips of female Augochlorini, dorsal views. **183,** *Corynura (Corynura) chilensis* (Spinola); **184,** *Corynurella mourei* n. sp.; **185,** *Rhectomia pumilla* Moure; **186,** *Rhinocorynura briseis* (Smith); **187,** *Neocorynura (Neocorynura) pubescens* (Friese); **188,** *Paroxystoglossa transversa* Moure; **189,** *Augochloropsis (Paraugochloropsis) metallica* (Fabricius); **190,** *Augochloropsis* sp. (=*Glyptochlora*); **191,** *Thectochlora alaris* (Vachal); **192,** *Augochlora (Augochlora)* sp.; **193,** *Augochlora (Mycterochlora) repandirostris* (Vachal); **194,** *Augochlora (Oxystoglossella)* sp.



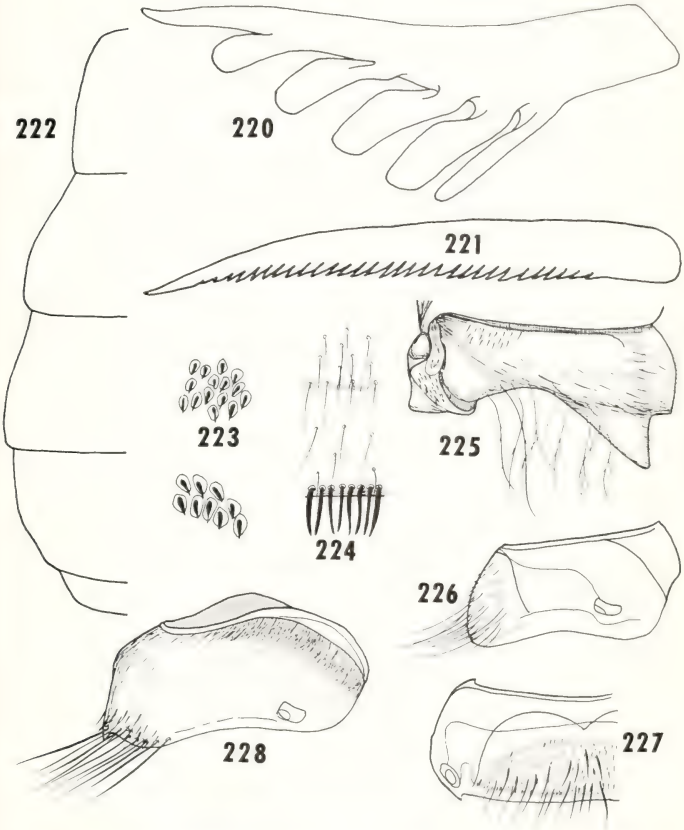
FIGS. **195-205.** Mesosomal structures of female Augochlorini. **195-198,** pronota and mesoscutal lips. **195-196,** *Megalopta genalis* Meade-Waldo (195, dorsal view; 196, lateral view); **197,** *Temnosoma smaragdinum* Smith, dorsal view; **198,** *Chlerogella elongaticeps* Michener, dorsal view. **199-200,** tegulae. **199,** *Augochloropsis (Paraugochloropsis) metallica* (Fabricius); **200,** *Temnosoma smaragdinum* Smith. **201,** apex of marginal cell of forewing of *Augochlorella striata* (Provancher). **202-205,** basitibial plates, anterior edges to left. **202,** *Corynura (Callochlora) chloris* (Spinola); **203,** *Andinaugochlora micheneri* n. sp.; **204,** *Augochloropsis (Paraugochloropsis) metallica* (Fabricius); **205,** *Megalopta genalis* Meade-Waldo.



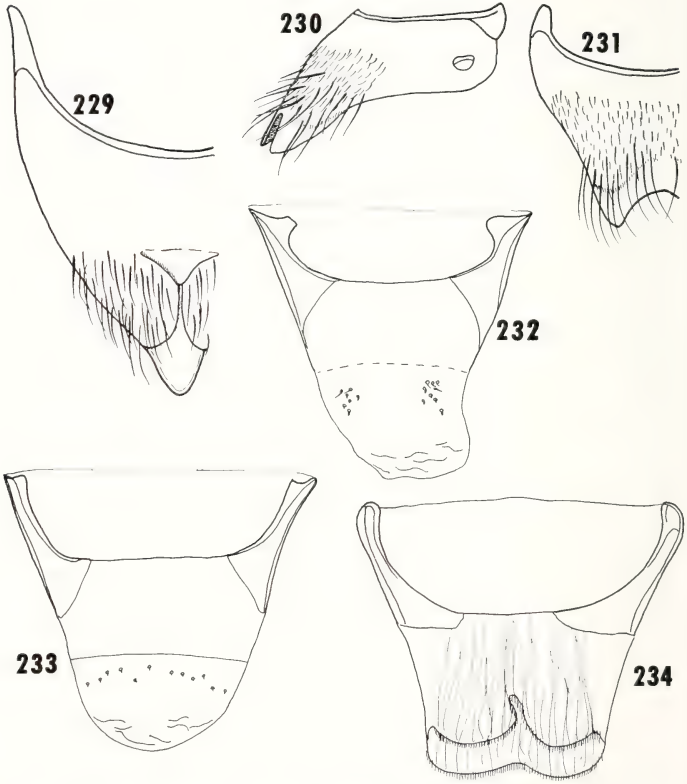
Figs. **206-212.** Inner hind tibial spurs of female Augochlorini. **206,** *Corynura (Corynura) chilensis* (Spinola); **207,** *Corynura (Corynura) corynoxaster* (Spinola); **208,** *Corynura (Callochlora) chloris* (Spinola); **209,** *Halictillus* sp.; **210,** *Rhinocorynura* sp.; **211,** *Neocorynura (Neocorynura) pubescens* (Friese); **212,** *Andinaugochlora micheneri* n. sp.



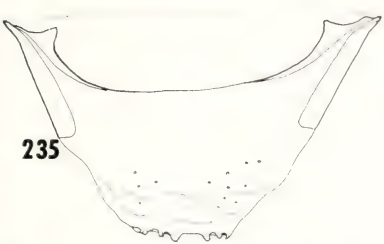
FIGS. 213-219. Inner hind tibial spurs of female Augochlorini. **213,** *Augochloropsis (Augochloropsis) ignita* (Smith); **214,** *Augochlora (Augochlora) nigrocyanea* (Cockerell); **215,** *Ceratalictus theia* (Schrottky); **216,** *Pereirapis* sp.; **217,** *Caenaugochlora (Ctenaugochlora) perpectinata* (Michener); **218,** *Megommation (Megaloptina)* sp.; **219,** *Ariphanarthra palpalis* Moure.

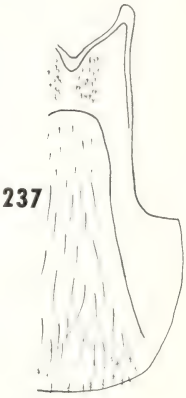


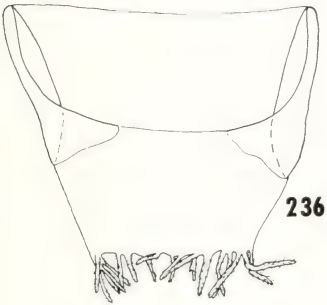
Figs. 220-228. Mesosomal and metasomal structures of Augochlorini. 220-221, inner hind tibial spurs of females. 220, *Megalopta genalis* Meade-Waldo; 221, *Temnosoma smaragdinum* Smith. 222, metasoma of *Neocorynura* (*Neocorynura*) *pubescens* (Friese) male, dorsal view. 223, scale-like setae of pseudopygidial area of *Augochlora* (*Augochlora*) *pura* (Say) female. 224, Apical setae (vibrissae) of metasomal tergum I of *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius) female. 225, Metasomal sternum I of *Augochlora* (*Augochlora*) sp., lateral view. 226-228, Metasomal terga VII of males. 226, *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius), lateral view; 227, *Augochloropsis* (*Augochloropsis*) *ignita* (Smith), posterior view; 228, *Ariphanarthra palpalis* Moure, posterior-lateral view.

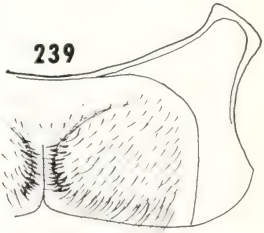


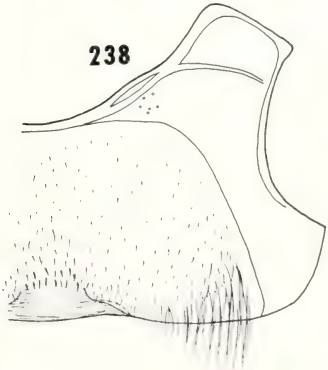
FIGS. **229-234.** Metasomal terga of Augochlorini. **229,** tergum VI of *Temnosoma smaragdinum* Smith female, dorsal view; **230-231,** tergum VII of *Temnosoma smaragdinum* Smith male (230, lateral view; 231, dorsal view). **232-234,** proctigers of males. **232,** *Temnosoma smaragdinum* Smith; **233,** *Ceratalictus theia* (Schrottky); **234,** *Rhinocorynura briseis* (Smith).



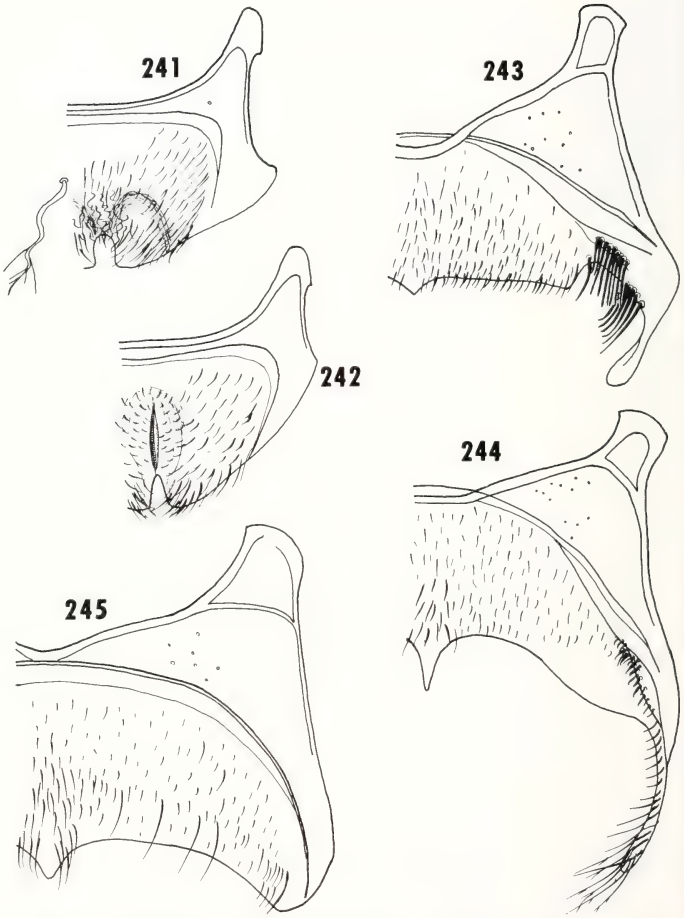




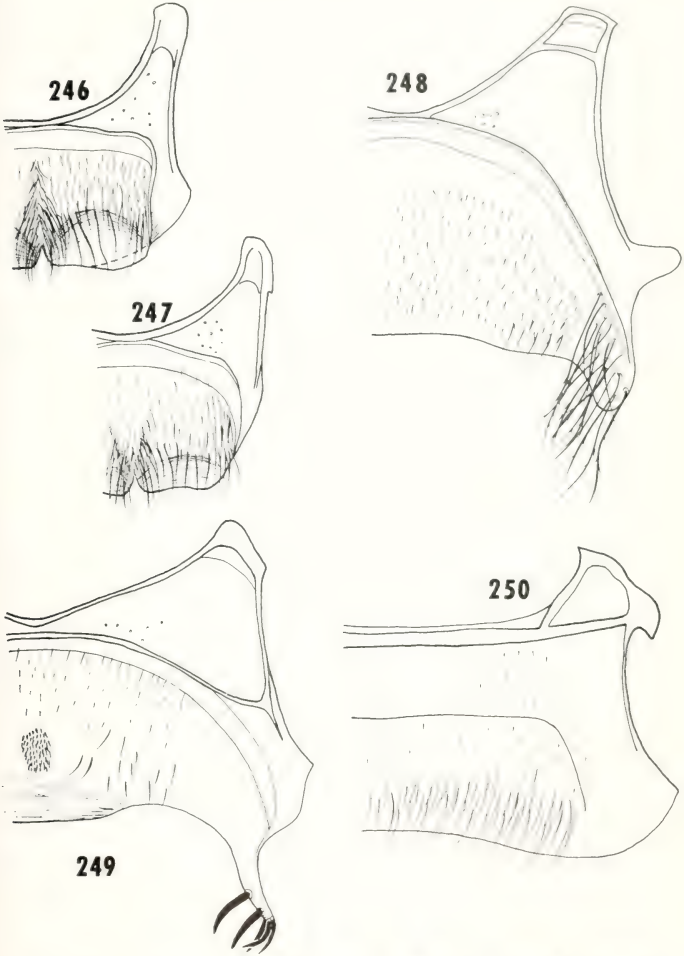




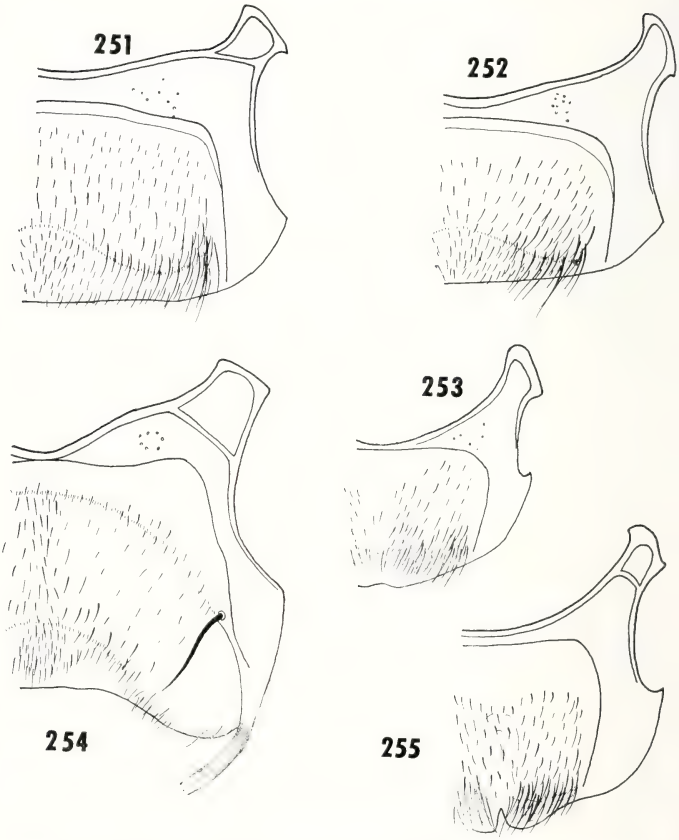
Figs. **235-240.** Metasomal structures of male Augochlorini. **235-236,** proctigers. **235,** *Augochloropsis (Paraugochloropsis) erato* (Holmberg); **236,** *Augochlora (Augochlora) pura* (Say). **237,** sternum II of *Neocorynura (Neocorynura) discolor knabiana* Cockerell. **238-240,** sterna of *Paroxystoglossa transversa* Moure (238, sternum IV; 239, sternum V; 240, sternum VI).



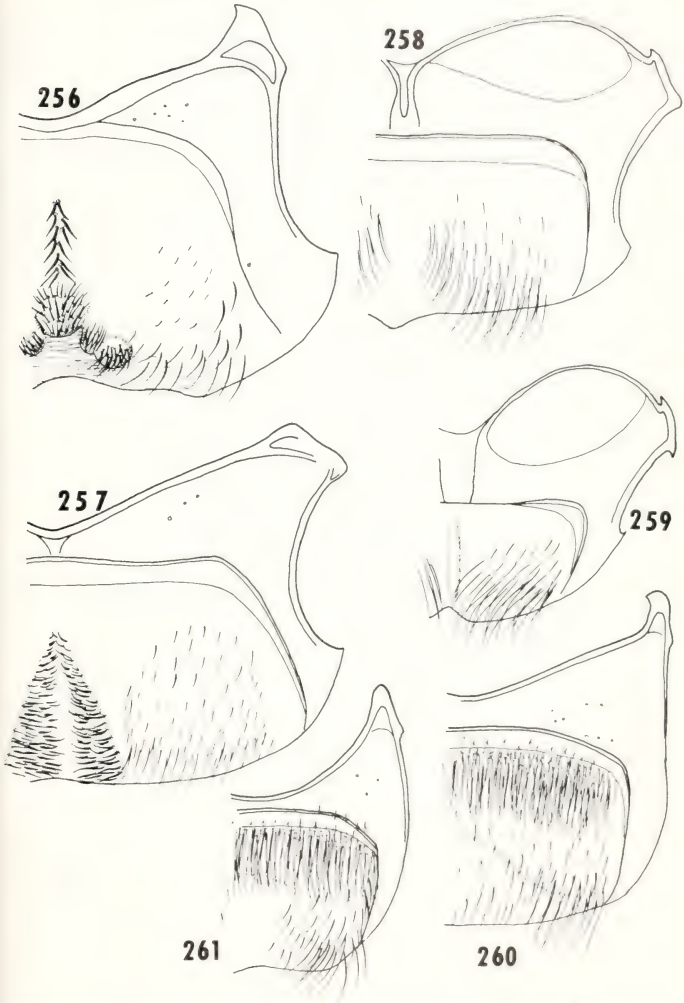
FIGS. 241-245. Metasomal sterna of male Augochlorini. **241,** sternum VI of *Andinaugochlora micheneri* n. sp.; **242,** sternum VI of *Chlerogas Pchlerogas* (Vachal); **243,** sternum IV of *Augochloropsis (Augochloropsis) ignita* (Smith); **244,** sternum IV of *Augochloropsis (Paraugochloropsis) metallica* (Fabricius); **245,** sternum IV of *Augochloropsis (Paraugochloropsis) chloera* (Moure) *(=Glyptobasia).*



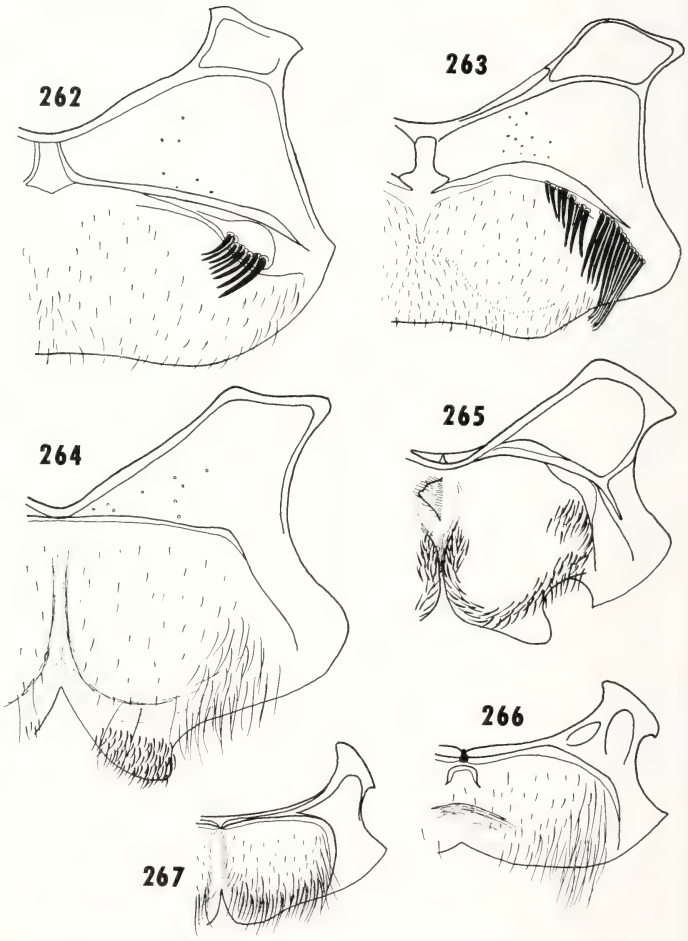
Figs. 246-250. Metasomal sterna of Augochlorini. 246, sternum VI of *Augochloropsis* (*Augochloropsis*) *ignita* (Smith) male; 247, sternum VI of *Augochloropsis* (*Augochloropsis*) *metallica* (Fabricius) male; 248, sternum IV of *Augochlorella gratiosa* Moure male; 249, sternum IV of *Thectochlora alaris* (Vachal) male; 250, sternum IV of *Augochlora* (*Augochlora*) *pura* (Say) female.



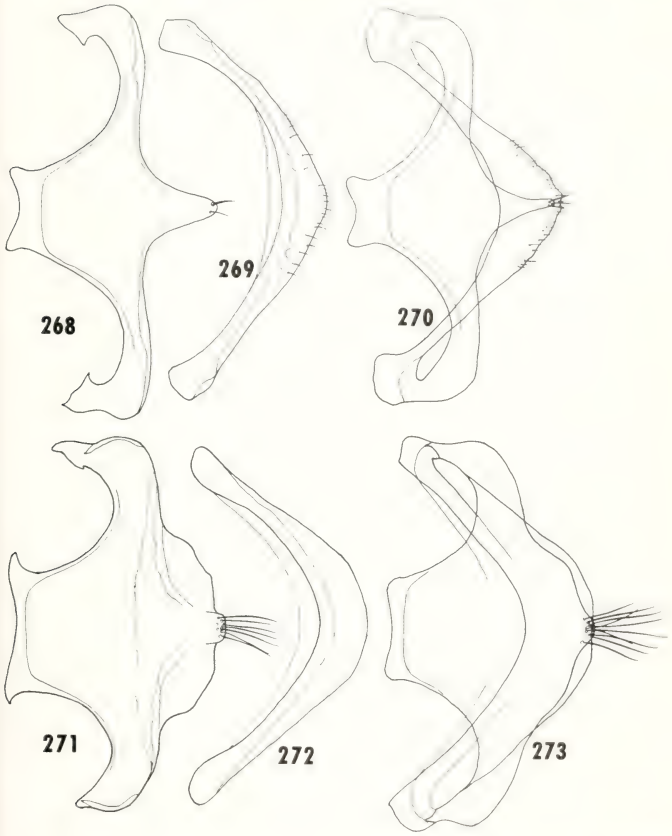
FIGS. **251-255.** Metasomal sterna of male Augochlorini. **251-253,** *Augochlora (Augochlora) pura* (Say) (251, sternum IV; 252, sternum V; 253, sternum VI); **254-255,** *Pereirapis* sp. (254, sternum IV; 255, sternum VI).



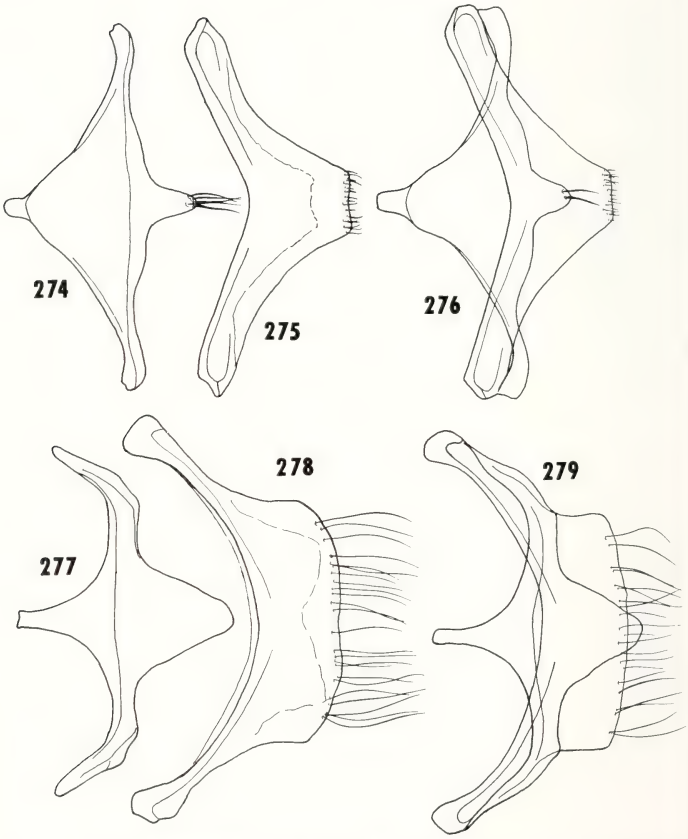
Figs. 256-261. Metasomal sterna of male Augochlorini. 256, sternum IV of *Caenaugochlora* (*Caenaugochlora*) *costaricensis* (Friese); 257-259, *Caenaugochlora* (*Caenaugochlora*) *perpectinata* (Michener) (257, sternum IV; 258, sternum V; 259, sternum VI); 260-261, *Temnosoma smaragdinum* Smith (260, sternumV; 261, sternum VI).



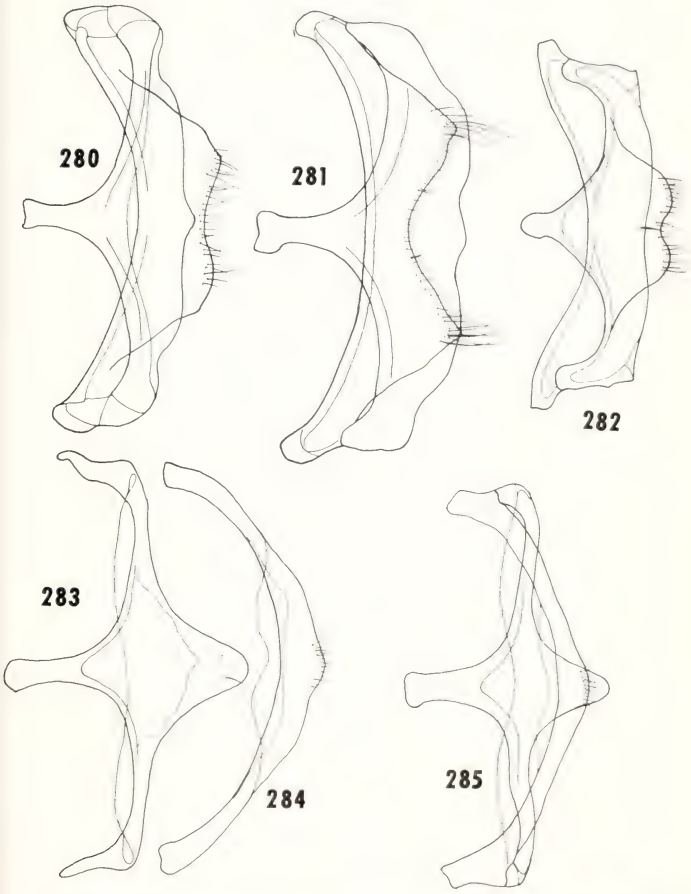
FIGS. **262-267.** Metasomal sterna of male Augochlorini. **262,** sternum IV of *Megommation (Megaloptina)* sp.; **263,** sternum IV of *Megommation (Megommation) insigne* (Smith); **264-267,** *Megulopta genalis* Meade-Waldo (264, sternum III; 265, sternum IV; 266, sternum V; 267, sternum VI).



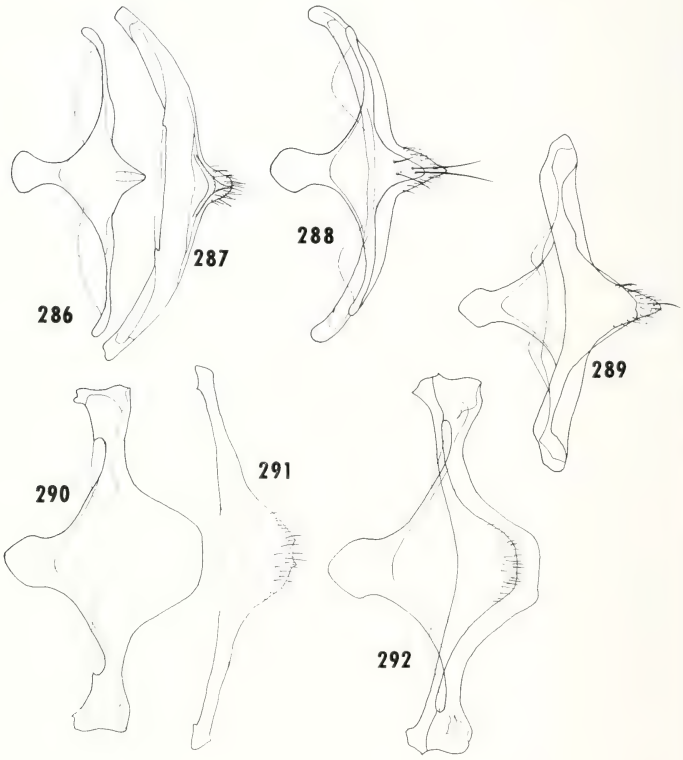
Figs. **268-273.** Metasomal sterna of male Augochlorini, anterior edges to left. **268-270,** *Corynura (Corynura) chilensis* (Spinola) (268, sternum VIII; 269, sternum VII; 270, sterna VII and VIII fused); **271-273,** *Corynura (Callochlora) calens* (Spinola) (271, sternum VIII; 272, sternum VII; 273, sterna VII and VIII fused).



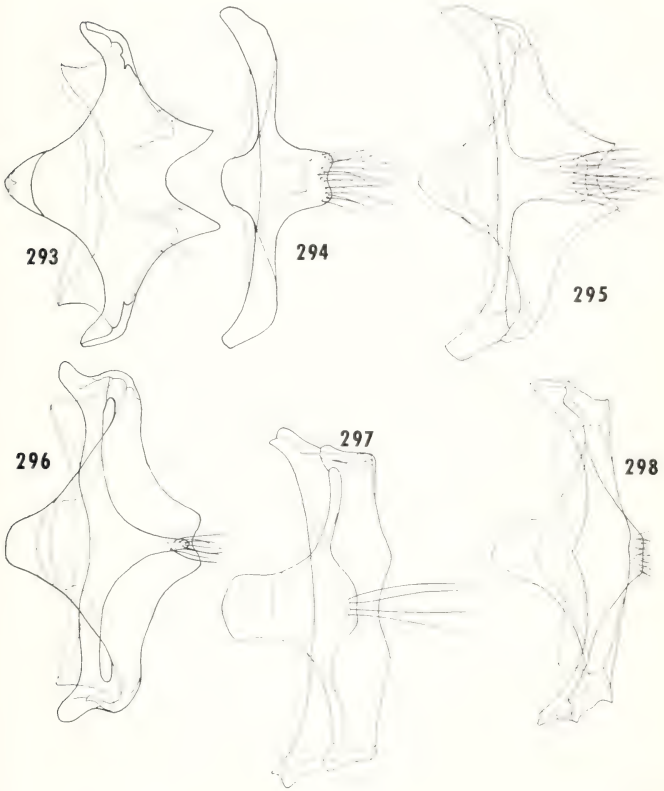
FIGS. **274-279.** Metasomal sterna of male Augochlorini, anterior edges to left. **274-276,** *Halictillus* sp. (274, sternum VIII; 275, sternum VII; 276, sterna VII and VIII fused); **277-279,** *Rhinocorynura briseis* (Smith) (277, sternum VIII; 278, sternum VII; 279, sterna VII and VIII fused).



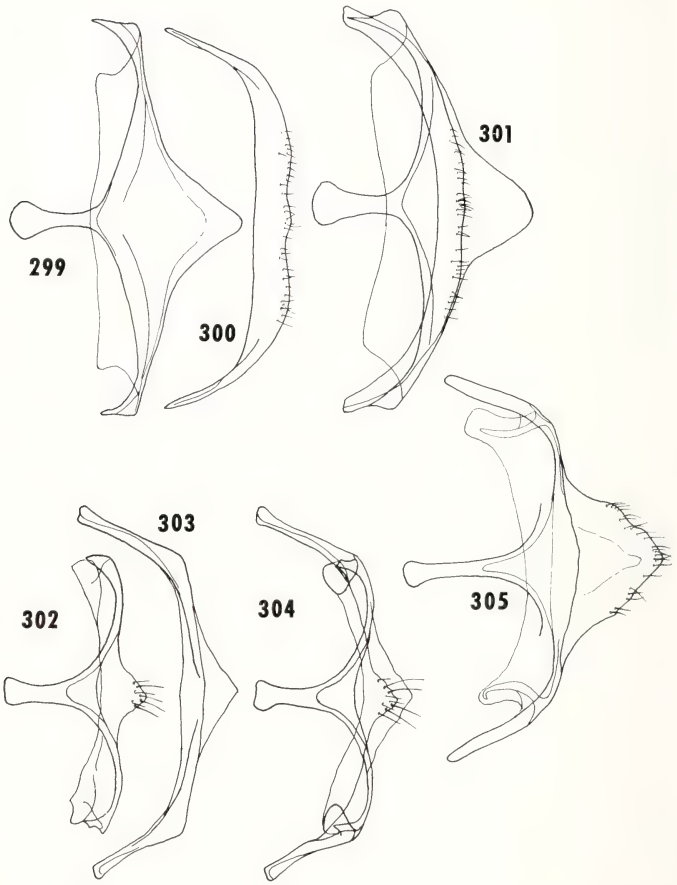
Figs. 280-285. Metasomal sterna of male Augochlorini, anterior edges to left. 280, sterna VII and VIII fused of *Rhinocorynura inflaticeps* (Ducke); 281, sterna VII and VIII fused of *Rhinocorynura* sp.; 282, sterna VII and VIII fused of *Corynurella mourei* n. sp.; 283-285, *Neocorynura (Neocorynura) pubescens* (Friese) (283, sternum VIII; 284, sternum VII; 285, sterna VII and VIII fused).



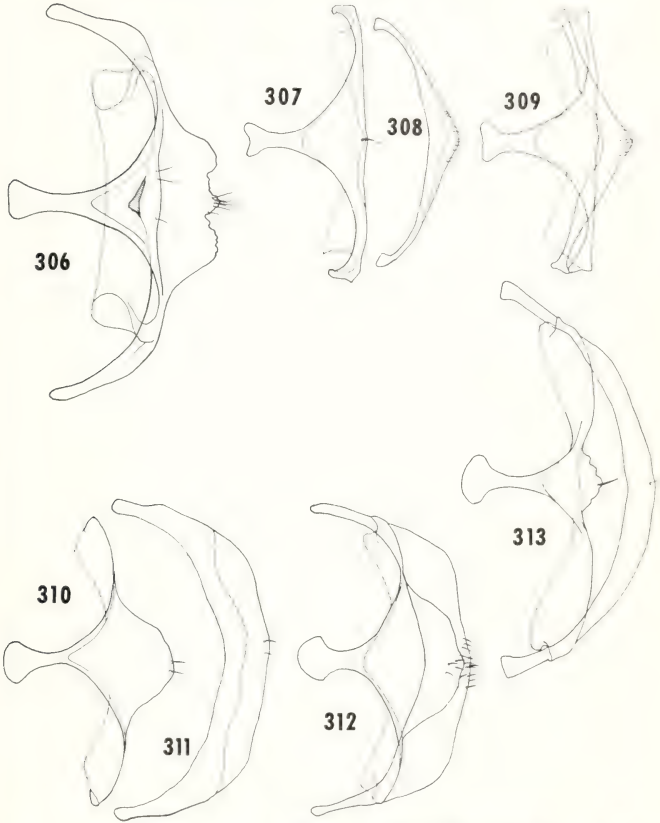
FIGS. 286-292. Metasomal sterna of male Augochlorini, anterior edges to left. **286-288,** *Paroxystoglossa transversa* Moure (286, sternum VIII; 287, sternum VII; 288, sterna VII and VIII fused); **289,** sterna VII and VIII fused of *Chlerogas ?chlerogas* (Vachal); **290-292,** *Andinaugochlora micheneri* n. sp. (290, sternum VIII; 291, sternum VII; 292, sterna VII and VIII fused).



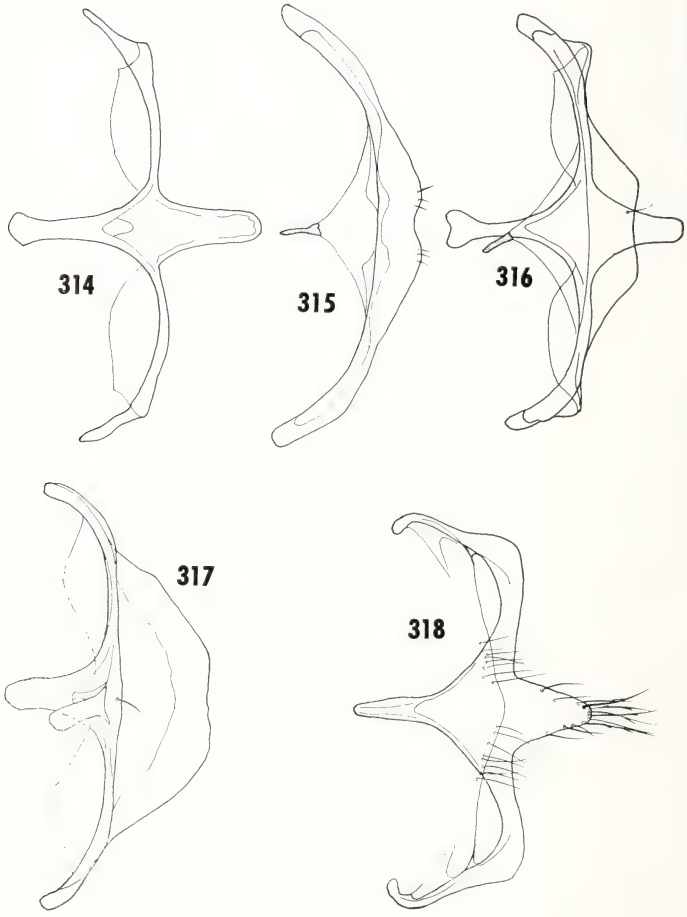
Figs. **293-298.** Metasomal sterna of male Augochlorini, anterior edges to left. **293-295,** *Augochloropsis (Paraugochloropsis) metallica* (Fabricius) (293, sternum VIII; 294, sternum VII; 295, sterna VII and VIII fused); **296,** sterna VII and VIII fused of *Augochloropsis (Augochloropsis) ignita* (Smith); **297,** sterna VII and VIII fused of *Augochloropsis (Paraugochloropsis) chloera* (Moure) *(=Glyptobasia);* **298,** sterna VII and VIII fused of *Augochlorodes turrifaciens* Moure.



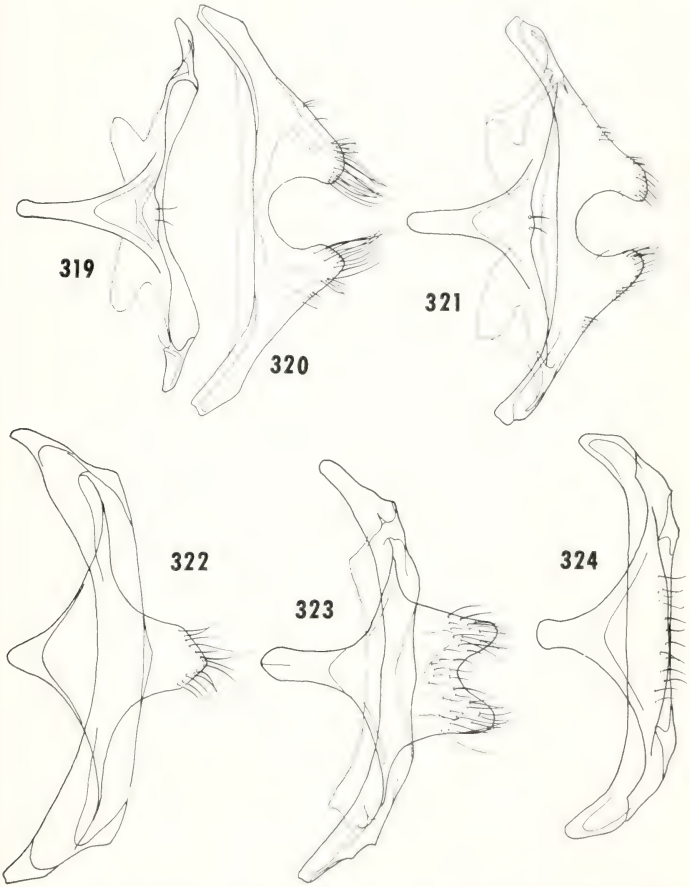
FIGS. **299-305.** Metasomal sterna of male Augochlorini, anterior edges to left. **299-301,** *Thectochlora alaris* (Vachal) (299, sternum VIII; 300, sternum VII; 301, sterna VII and VIII fused); **302-304,** *Augochlora (Augochlora) pura* (Say) (302, sternum VIII; 303, sternum VII; 304, sterna VII and VIII fused); **305,** sterna VII and VIII fused of *Augochlora (Oxystoglossella) cordiaefloris* (Cockerell).



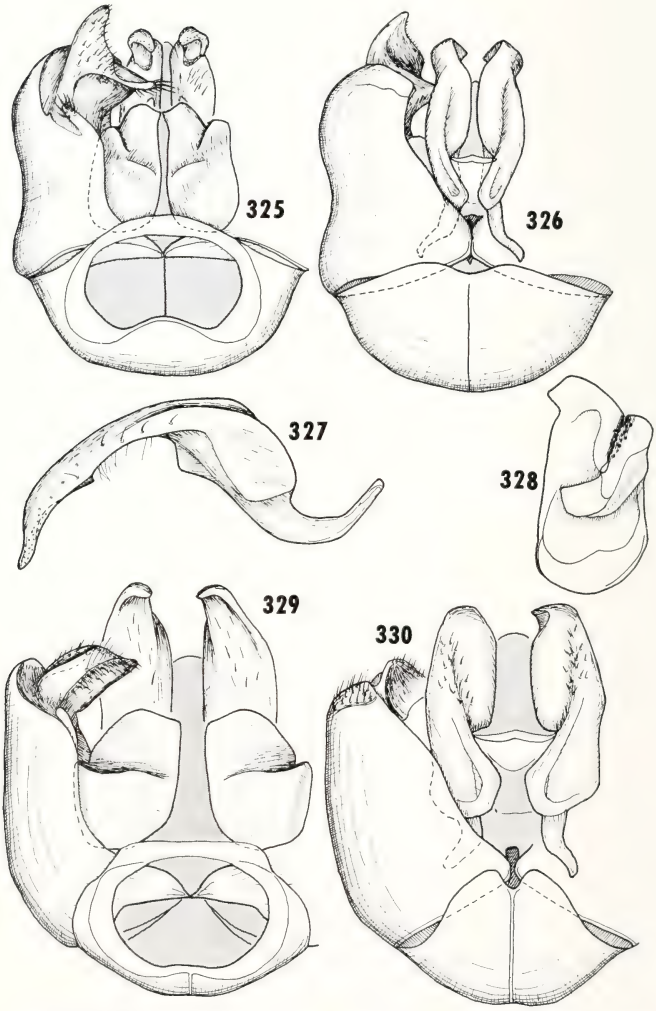
Figs. 306-313. Metasomal sterna of male Augochlorini, anterior edges to left. **306,** sterna VII and VIII fused of *Augochlora* (*Mystrochlora*) *repandirostris* (Vachal); **307-309,** *Augochlorella striata* (Provancher) (307, sternum VIII; 308, sternum VII; 309, sterna VII and VIII fused); **310-312,** *Ceratalictus zhena* (Schrottky) (310, sternum VIII; 311, sternum VII; 312, sterna VII and VIII fused); **313,** sterna VII and VIII fused of *Pereirapis* sp.



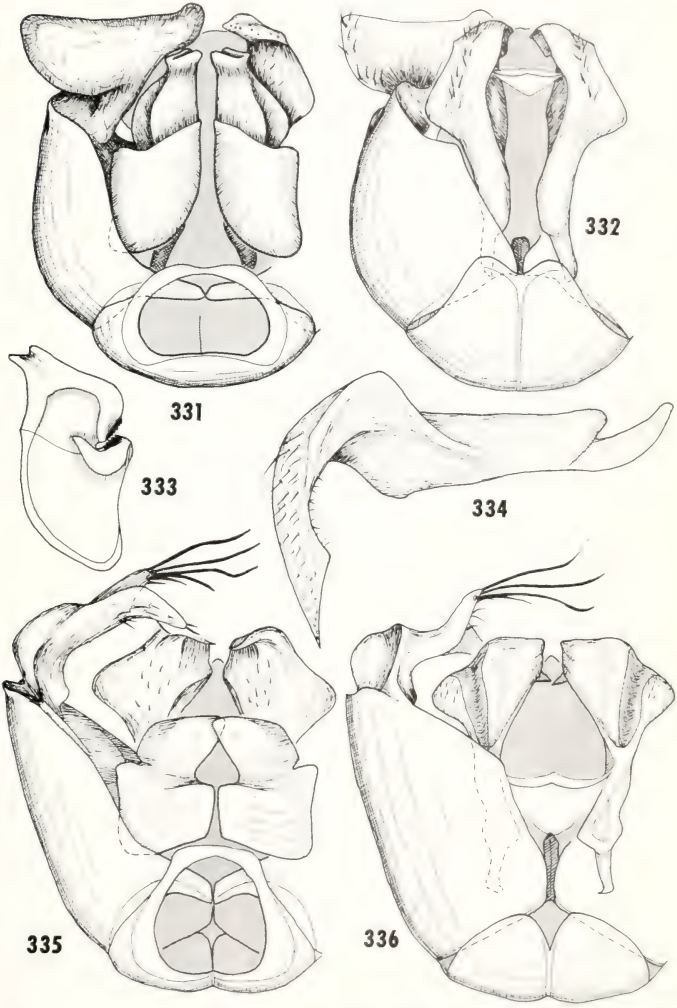
FIGS. **314-318.** Metasomal sterna of male Augochlorini, anterior edges to left. **314-316,** *Caenaugochlora (Caenaugochlora) costaricensis* (Friese) (314, sternum VIII; 315, sternum VII; 316, sterna VII and VIII fused); **317,** sterna VII and VIII fused of *Caenaugochlora (Ctenaugochlora) perfectinata* (Michener); **318,** sterna VII and VIII fused of *Temnosoma smaragdinum* Smith.



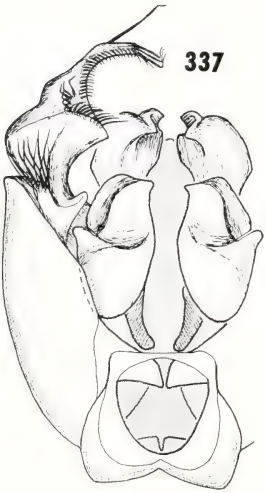
Figs. **319-324.** Metasomal sterna of male Augochlorini, anterior edges to left. **319-321,** *Megalopta genalis* Meade-Waldo (319, sternum VIII; 320, sternum VII; 321, sterna VII and VIII fused); **322,** sterna VII and VIII fused of *Megommation* (*Megaloptima*) sp.; **323,** sterna VII and VIII fused of *Megommation* (*Megommation*) *insigne* (Smith); **324,** sterna VII and VIII fused of *Ariphanarthra palpalis* Moure.

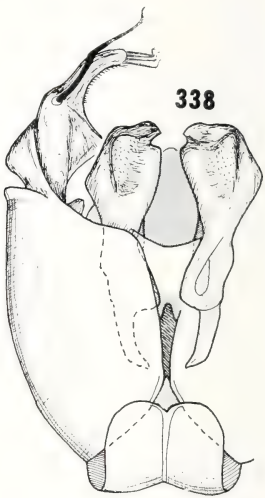


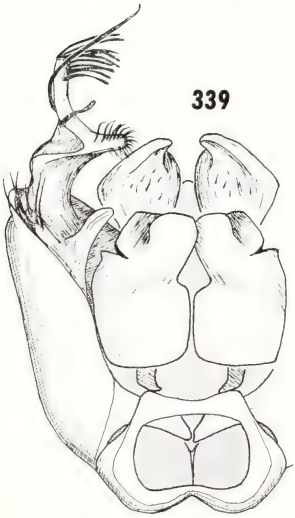
FIGS. **325-330.** External genitalia of male Augochlorini. **325-328,** *Corynura (Corynura) chilensis* (Spinola) (325, ventral view; 326, dorsal view; 327, penis valve, lateral view; 328, volsella, inner view); **329-330,** *Corynura (Callochlora) chloris* (Spinola) (329, ventral view; 330, dorsal view).



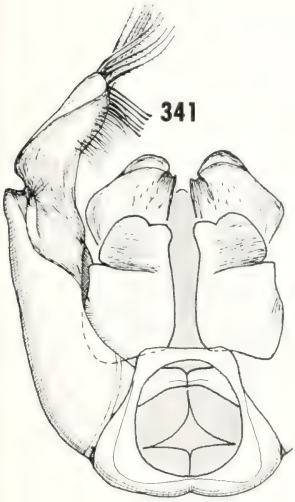
Figs. **331-336.** External genitalia of male Augochlorini. **331-334,** *Halictillus* sp. (331, ventral view; 332, dorsal view; 333, volsella, inner view; 334, penis valve, lateral view); **335-336,** *Corynurella mourei* n. sp. (335, ventral view; 336, dorsal view).

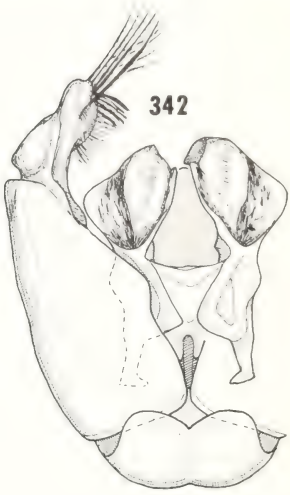


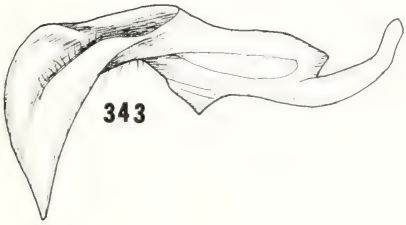




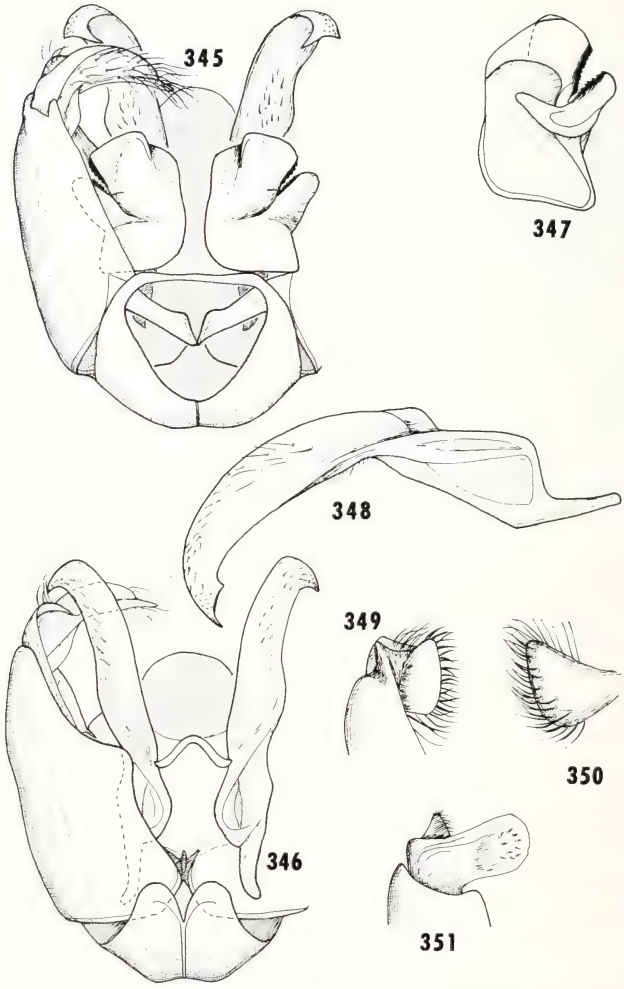
FIGS. **337-340.** External genitalia of male Augochlorini. **337-338,** *Rhinocorynura* sp. (337, ventral view; 338, dorsal view); **339-340,** *Rhinocorynura inflaticeps* (Ducke) (339, ventral view; 340, penis valve, dorsal view).



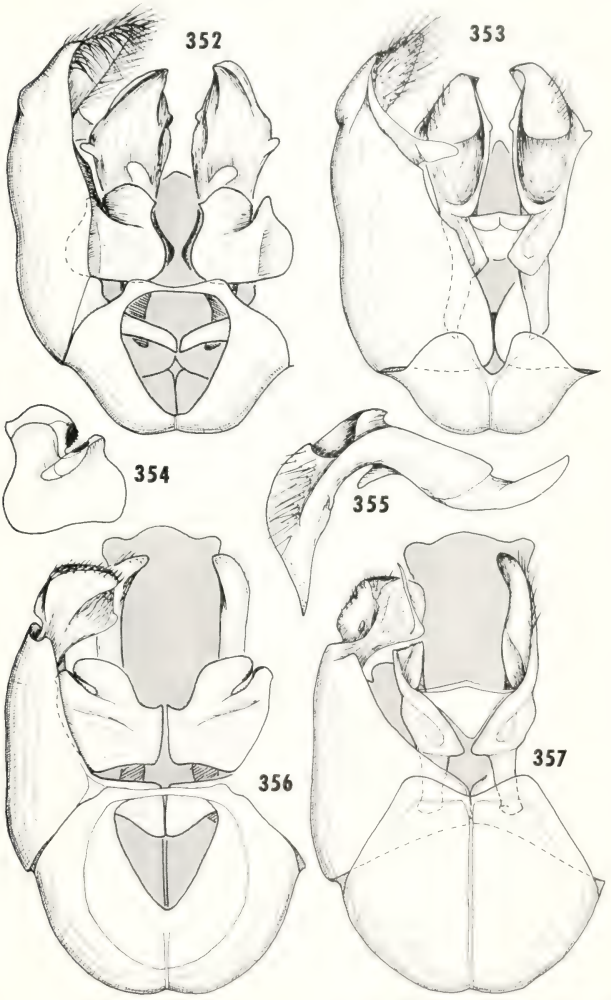




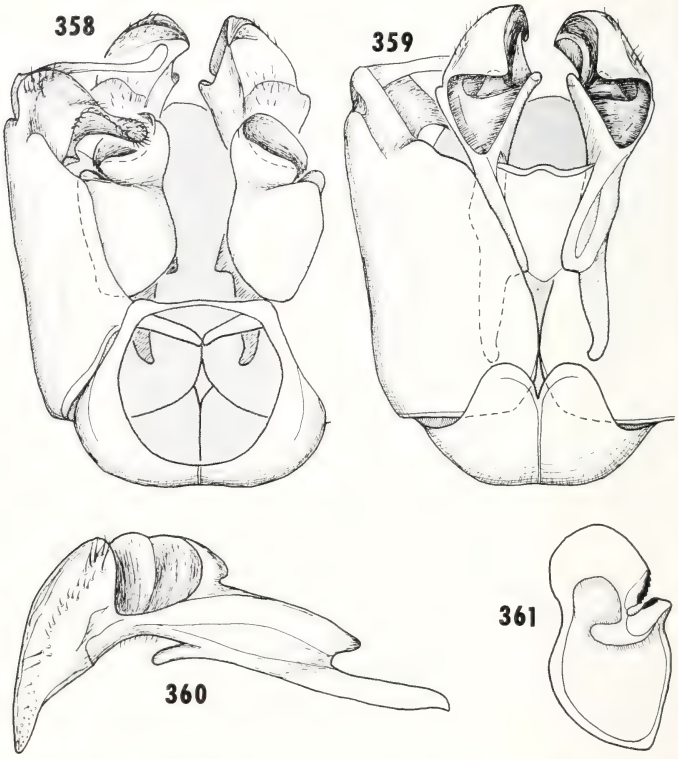
Figs. **341-344.** External genitalia of *Rhinocorynura briseis* (Smith) male. **341,** ventral view; **342,** dorsal view; **343,** penis valve, lateral view; **344,** volsella, inner view.



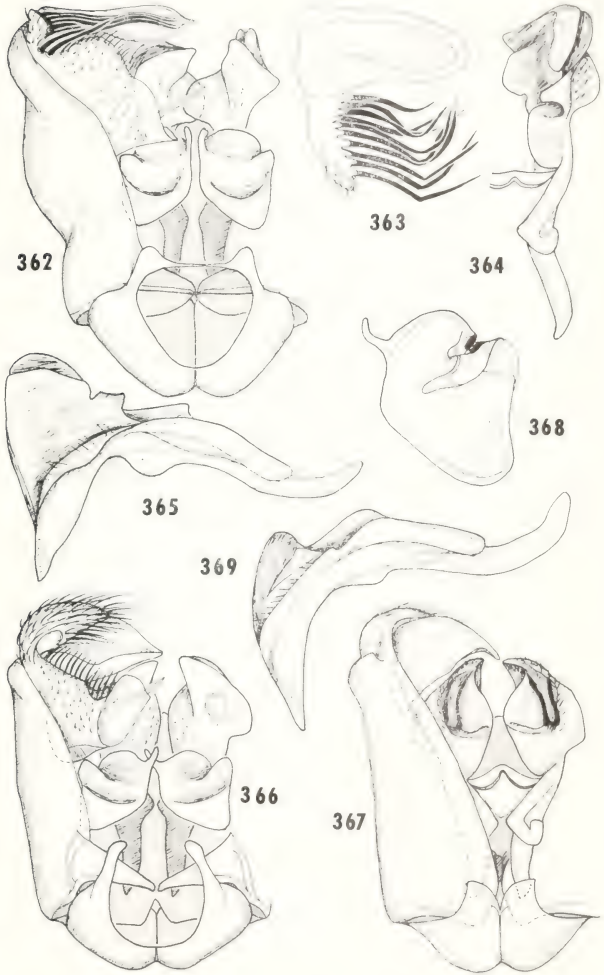
FIGS. **345-351.** External genitalia of male Augochlorini. **345-348,** *Neocorynura (Neocorynura) pubescens* (Friese) (345, ventral view; 346, dorsal view; 347, volsella, inner view; 348, penis valve, lateral view); **349-351,** *Neocorynura (Neocorynuroides) rhytis* (Vachal) (349, gonostylus, ventral view; 350, gonostylus, inner view; 351, gonostylus, dorsal view).



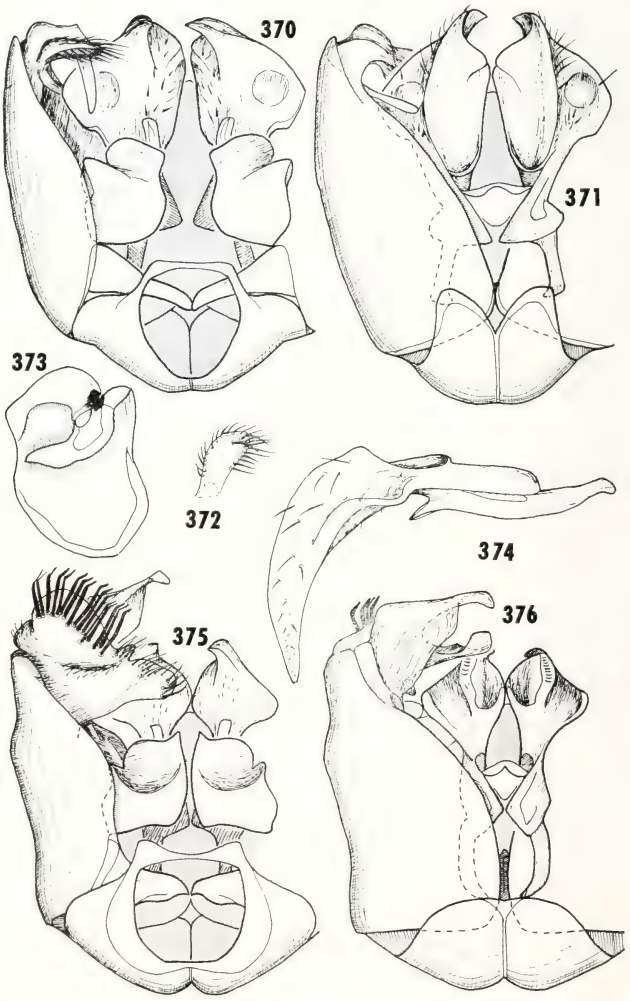
Figs. **352-357.** External genitalia of male Augochlorini. **352-355.** *Paroxystoglossa transversa* Moure (352, ventral view; 353, dorsal view; 354, volsella, inner view; 355, penis valve, lateral view); **356-357.** *Chlerogas Schlerogas* (Vachal) (356, ventral view; 357, dorsal view).



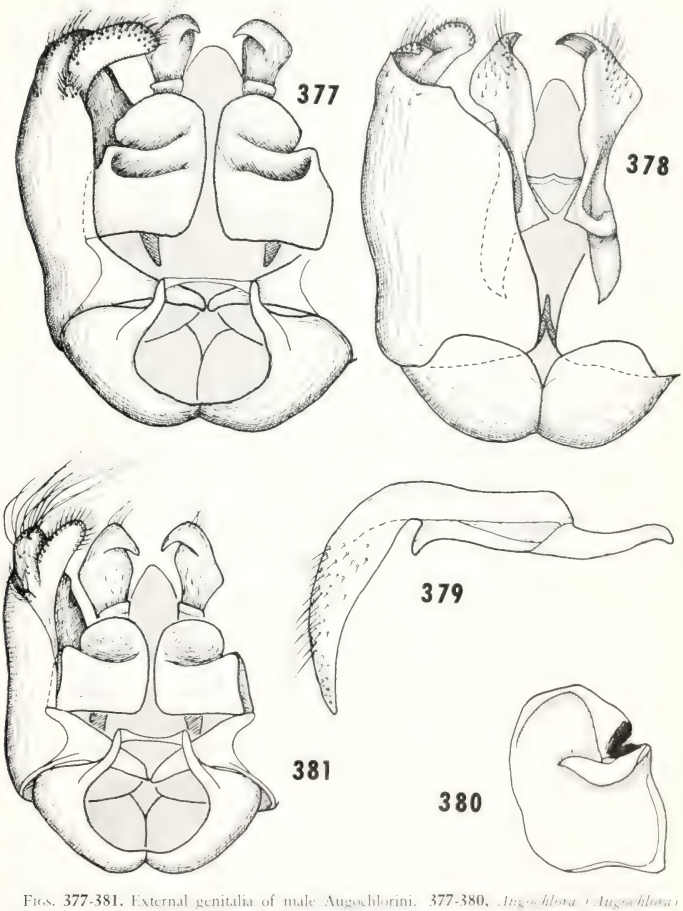
FIGS. 358-361. External genitalia of *Andinaugochlora micheneri* n. sp. male. **358,** ventral view; **359,** dorsal view; **360,** penis valve, lateral view; **361,** volsella, inner view.



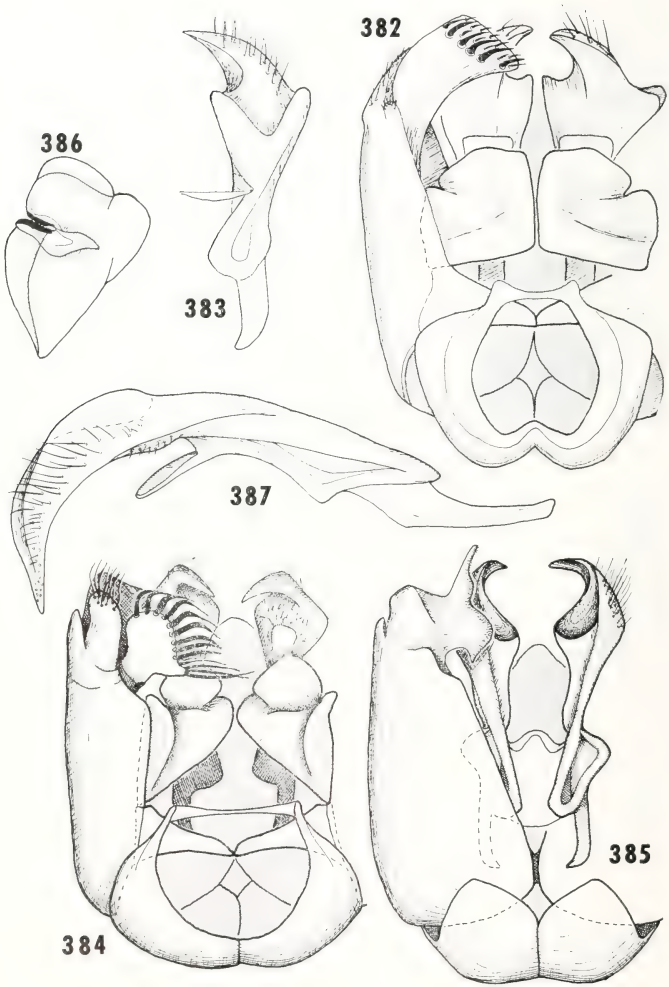
Figs. 362-369. External genitalia of male Augochlorini. 362-365, *Augochloropsis* (*Augochloropsis*) *ignita* (Smith) (362, ventral view; 363, gonostylus, apical view; 364, penis valve, dorsal view; 365, penis valve, lateral view); 366-369, *Augochloropsis* (*Paraugochloropsis*) *metallica* (Fabricius) (366, ventral view; 367, dorsal view; 368, volsella, inner view; 369, penis valve, lateral view).



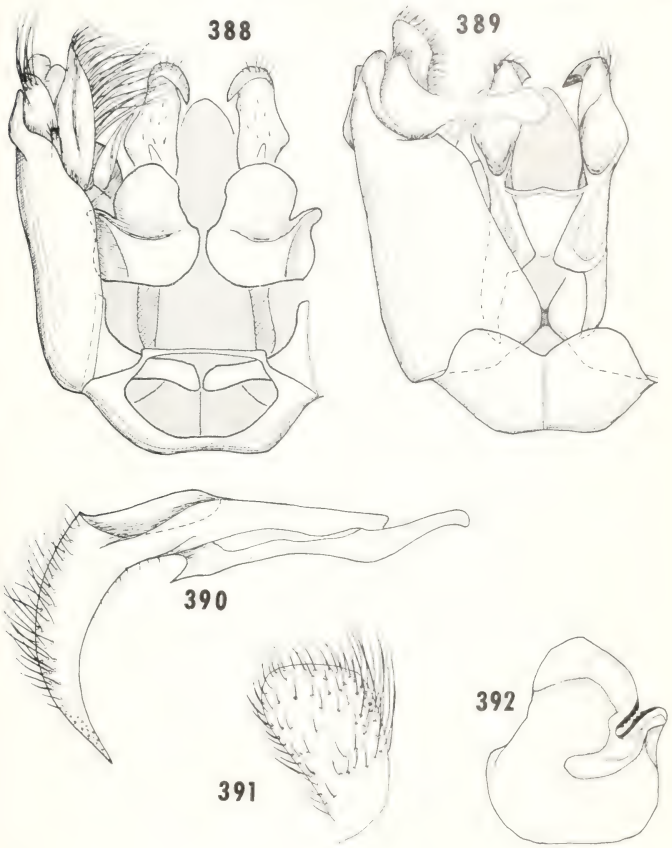
FIGS. **370-376.** External genitalia of male Augochlorini. **370-374,** *Thectochlora alaris* (Vachal) (370, ventral view; 371, dorsal view; 372, gonostylus, inner view; 373, volsella, inner view; 374, penis valve, lateral view); **375-376,** *Augochlorodes turrifaciens* Moure (375, ventral view; 376, dorsal view).



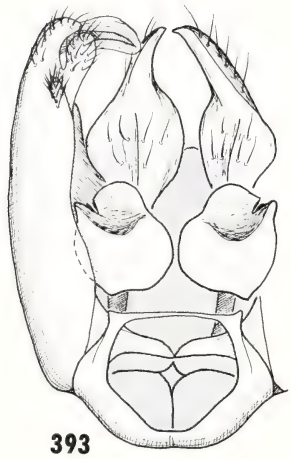
Figs. **377-381.** External genitalia of male Augochlorini. **377-380.** *Augochlora* (*Augochlorella*) *pura* (Say) (377, ventral view; 378, dorsal view; 379, penis valve, lateral view; 380, volsella, inner view); **381,** ventral view, *Augochlora* (*Oxystoglossella*) *cordiaefloris* Cockerell.

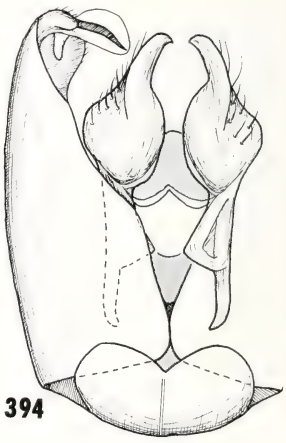


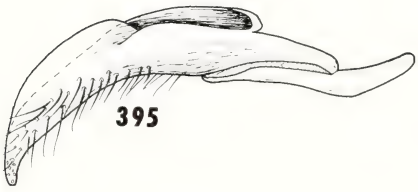
FIGS. **382-387.** External genitalia of male Augochlorini. **382-383,** *Augochlora (Mycterochlora) repandirostris* (Vachal) (382, ventral view; 383, penis valve, dorsal view); **384-387,** *Augochlorella striata* (Provancher) (384, ventral view; 385, dorsal view; 386, volsella, inner view; 387, penis valve, lateral view).

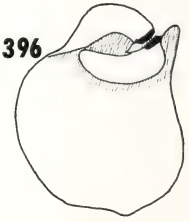


Figs. 388-392. External genitalia of *Cevatalictus theia* (Schrottky) male. 388, ventral view; 389, dorsal view; 390, penis valve, lateral view; 391, gonostylus, inner view; 392, volsella, inner view.

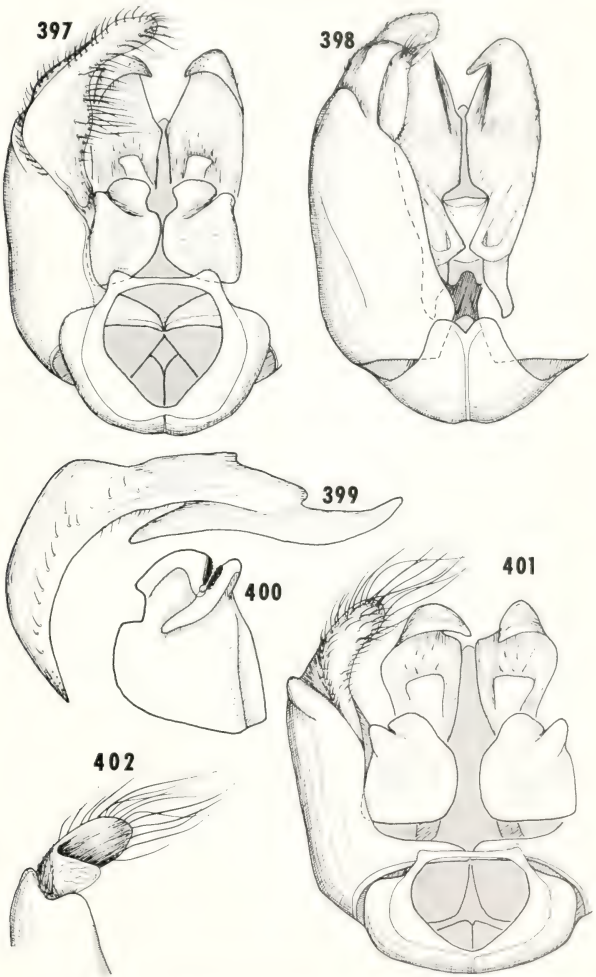




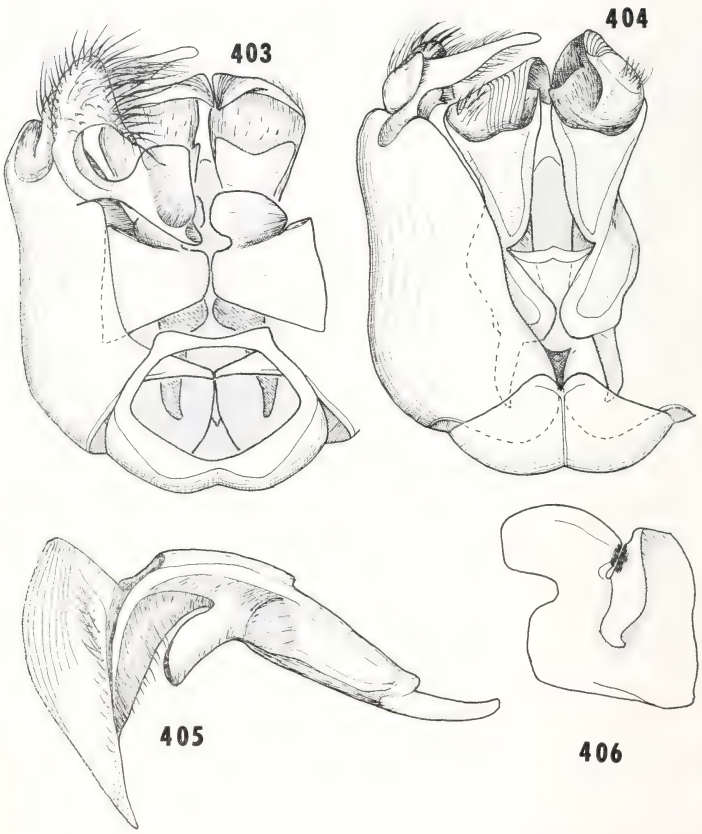




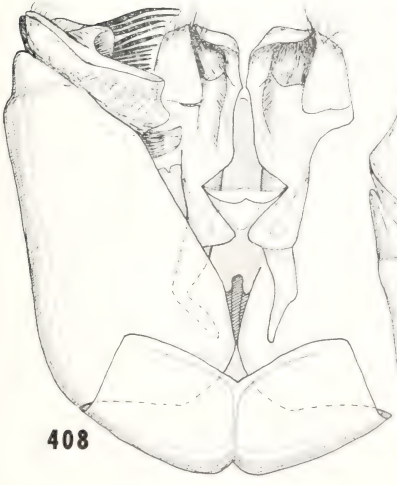
FIGS. **393-396.** External genitalia of *Pereirapis* sp. male. **393,** ventral view, **394,** dorsal view; **395,** penis valve, lateral view; **396,** volsella, inner view.



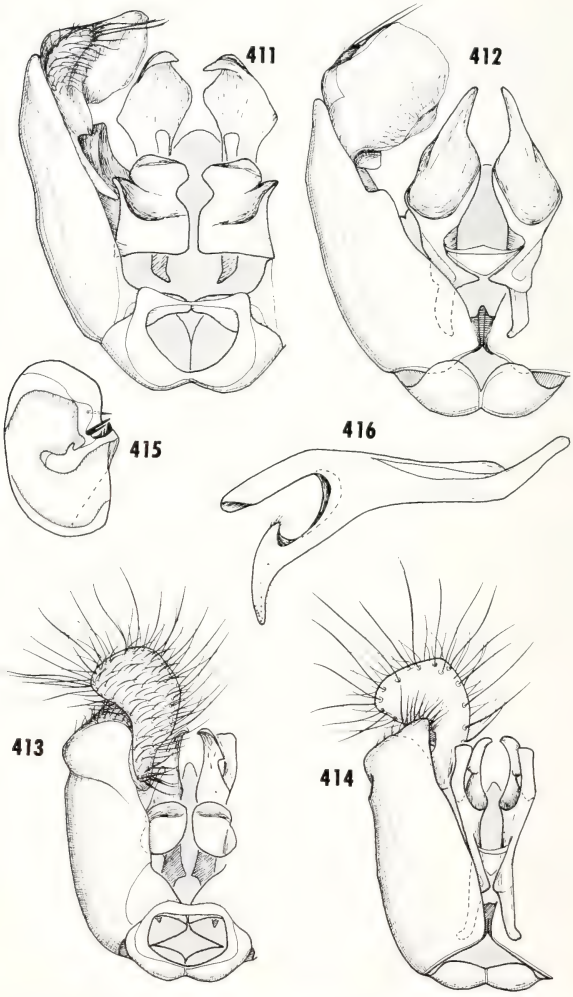
Figs. **397-402.** External genitalia of male Augochlorini. **397-400,** *Caenaugochlora (Caenaugochlora) costaricensis* (Friese) (397, ventral view; 398, dorsal view; 399, penis valve, lateral view; 400, volsella, inner view); **401-402,** *Caenaugochlora (Ctenaugochlora) perpectinata* (Michener) (401, ventral view; 402, gonostylus, dorsal view).



FIGS. 403-406. External genitalia of *Megalopta genalis* Meade-Waldo male. **403,** ventral view; **404,** dorsal view; **405,** penis valve, lateral view, crest expanded; **406,** volsella, inner view.



Figs. **407-410.** External genitalia of male Augochlorini. **407-408,** *Megommation (Megommation) insigne* (Smith) (407, ventral view; 408, dorsal view). **409-410,** *Megommation (Megaloptina)* sp. (409, ventral view; 410, dorsal view).



FIGS. **411-416.** External genitalia of male Augochlorini. **411-412,** *Ariphanarthra palpalis* Moure (411, ventral view; 412, dorsal view); **413-416,** *Temnosoma smaragdinum* Smith (413, ventral view; 414, dorsal view; 415, volsella, inner view; 416, penis valve, lateral view).

DISCUSSION

Estimation of relationships. As pointed out by Sokal and Sneath (1963), two types of relationship among taxa are of interest to systematists: *phenetic* relationship which deals with the overall similarity of organisms, and *cladistic* relationship which deals with paths of evolutionary lineage. In the absence of fossils, both types of relationship are ascertained from the same data, by examining contemporary organisms.

All genera of the Augochlorini represent, I believe, "natural" taxa in the usual cladistic sense. That is, they are monophyletic, the species in each genus presumably having arisen by cleavage of a common stem species. I arrived at this conclusion after examining many species; in each genus the species are linked by common characteristics which in my opinion are indicative of common ancestry. The complex external male genitalia provide especially important evidence, as species in each genus have similar genitalia but the basic structural plan for each genus is usually distinctive.

Of course, the genera differ as to the amount of phenetic variability their species exhibit around common generic structural plans. Some genera are "cohesive" or "closely-knit" in that their species are very similar in all characters; these genera frequently possess distinctive characters which readily separate them from all other genera. Other genera are less cohesive in that their species are more variable; these genera often are less distinctly separated from phenetically related genera. However, if male genitalia are taken into account, generic limits of even loosely-knit genera are rather easy to recognize in comparison with many groups of insects. In only the *Rhinocorynura* and *Megaloptidia* groups of genera (as delimited below) are the genera so similar or poorly known that generic limits proved difficult to ascertain and are somewhat arbitrarily drawn.

If one accepts as a working hypothesis that the genera recognized in this paper are "natural" cladistic units, they may be used as operational taxonomic units (see Sokal and Sneath, 1963) in phenetic and cladistic studies to determine relationships among genera and possible evolutionary paths followed by the Augochlorini. A numerical analysis was undertaken to aid in ascertaining overall phenetic similarities among augochlorine genera, using a large number of characters, equally weighted. (See the section on Methods for further details and Sokal and Sneath, 1963, for the special terminology of numerical taxonomy.) The validity of this analysis depends upon the accuracy of the character coding and to some extent on the choice of characters. Some characters were easily coded (such as the epistomal sulcus and the hypostomal length) and thus are ideally suited for numerical analysis, while others could not be coded satisfactorily (particularly characters of the metasomal sterna and the genitalia), and their contributions to overall phenetic similarity are poorly indicated in the numerical analysis.

Estimations of cladistic relationship take into account convergence and direction of evolution, and disregard the rate of evolution and thus, theoretically, the degree of phenetic similarity. When my estimate of cladistic relationship differs from the estimate of phenetic affinity provided by the numerical analysis, it is usually due to my weighting of characters that appear to be of importance due to their complexity, for instance the galeal comb and the male genitalia. The generic groups denoted below are a product of both phenetic and cladistic analysis. While the numerical analysis was used as an aid in formulating these groups, often providing welcome support for groups recognized before the numerical study was made, the groupings accepted are not all justified by the analysis and those that are recognized are not joined at the same phenon levels. On the other hand, no groups were formulated by clustering very dissimilar taxa (as indicated by the numerical analysis) because they were linked by some common character that I deemed of special cladistic importance.

Summary of the numerical analysis. Cluster analyses based on both the correlation and distance coefficients created initial clusters which largely agree with my previous concepts as to what constitute "natural" cladistic and phenetic groupings. Subsequent levels of clustering, as shown in the phenograms (Figs. 417-418) are not reliable; relationships which are evident in the correlation and distance matrices are frequently hidden in the phenograms. The two cluster analyses largely agree between themselves on initial groupings but frequently disagree as to larger (i.e. subsequent) clusters. The analysis based upon correlation coefficients (Fig. 418) better delimits groups that were apparent to me before the analysis, but the analysis based upon distance coefficients (Fig. 417) sets distinctly different genera (e.g., *Temnosoma*) further apart from the other genera. The cophenetic value of the distance phenogram is .91 and of the correlation phenogram, .85, each with its own matrix.

Generic groups. Most of the genera of the Augochlorini fall into seven more-or-less well-defined generic groups. Relationships among the generic groups are for the most part difficult to interpret.

CORYNURA GROUP. *Corynura, Callochlora,* and *Halictillus* form a cohesive group of South Temperate species, most of which resemble nonaugochlorine halictines. The form of the mouthparts, galeal comb, largely dull coloring, and the striking resemblance of *Halictillus* to *Dialictus* (except for the genitalia and hidden sterna) suggest that the *Corynura* group may be important in ascertaining cladistic relationship of the Augochlorini to other groups of bees. The phenograms suggest that *Halictillus* should perhaps be considered only subgenerically distinct from *Corynura,* but the numerical analysis does not adequately take into consideration the form of the male genitalia, which is quite different in *Halictillus* from that in *Corynura* and *Callochlora.*

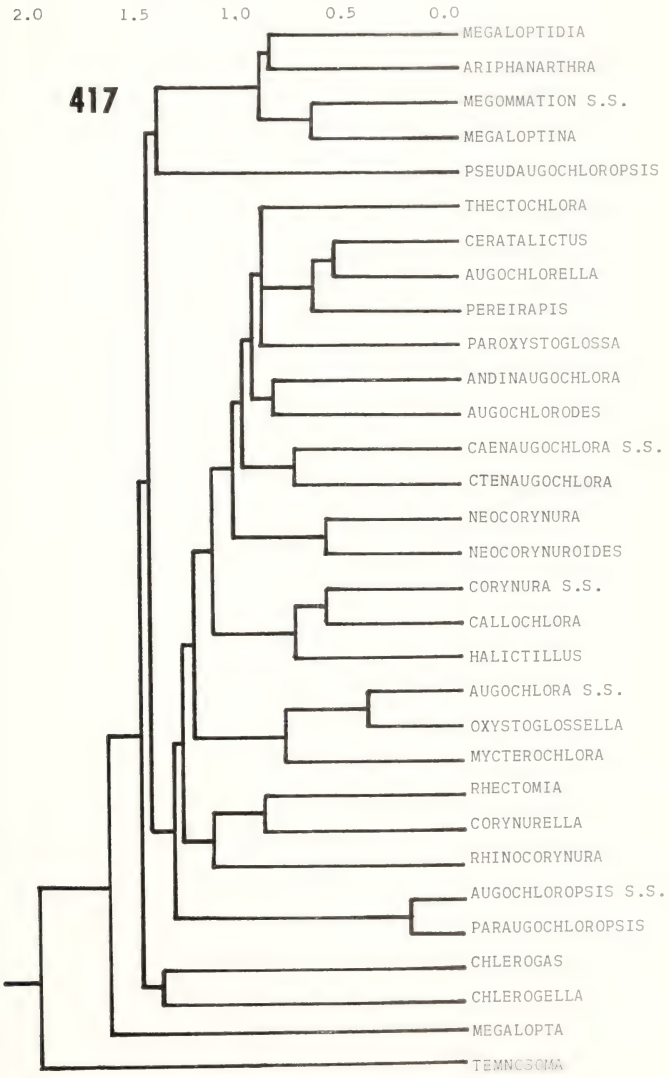


Fig. 417. Phenogram of the Augochlorini based upon the distance matrix.

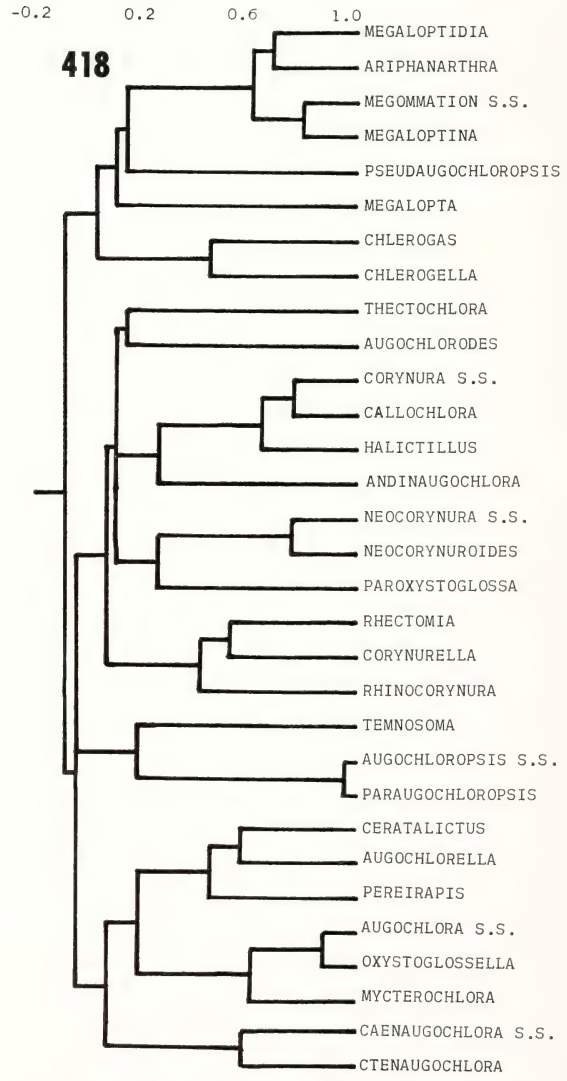


FIG. 418. Phenogram of the Augochlorini based upon the correlation matrix.

RHINOCORYNURA GROUP. *Rhinocorynura*, *Corynurella*, and *Rhectomia* comprise another cohesive group of largely dull bees, linked by common plans of mouthparts and male genitalic and hidden sternal and tergal structure. A cladistic relationship to the *Corynura* group is suggested by a number of characters, especially the mouthparts; the *Rhinocorynura* group occupies a range on the northern border of that of the *Corynura* group. *Rhectomia*, like *Halictillus*, superficially resembles *Dialictus*. Both distance and correlation phenograms recognize the *Rhinocorynura* group, but both separate it slightly from the *Corynura* group. However, *Rhectomia* is most similar outside its group in the distance matrix to *Corynura* (1.034), and in the correlation matrix to *Halictillus* (0.335); *Corynurella* is next most similar outside its group in the correlation matrix to *Halictillus* (it is most similar to *Chlerogella*), although it is more distant in the distance matrix (1.231 to *Corynura*); and *Rhinocorynura* is most similar outside its group in the correlation matrix (0.165) and next most similar in the distance matrix (1.310) to *Corynura*. These values suggest a greater similarity to the *Corynura* group than either of the phenograms implies.

NEOCORYNURA GROUP. *Neocorynura*, *Neocorynuroides*, *Paroxystoglossa*, *Andinaugochlora* and *Chlerogas* form a loosely knit group. *Neocorynura* is the largest and most widespread genus of the group, its range overlapping all of the others, and consequently is the genus with which the others of the group should be compared.

The Peruvian genus *Chlerogas* resembles at least one species of *Neocorynura* in its bituberculate scutellum; and the genitalia, with the narrow penis valves, are also similar; *Chlerogas* could not be compared as to its mouthparts and characters of the female, and consequently its relationships are inconclusive. Both phenograms indicate that *Chlerogas* and *Chlerogella* are most similar to each other; this is probably due to convergence in the lengthening of the head and the large number of "no comparisons" for both genera, since each is known from only one sex. Both matrices suggest a close similarity of *Chlerogas* to *Andinaugochlora*, closest in the distance matrix (1.111) and next closest in the correlation matrix (9.262) (after *Chlerogella*).

The Andean genus *Andinaugochlora* resembles Andean species of *Neocorynura* in general appearance as well as in the mouthparts (especially the small galeal comb) and long male antennae, but has quite different male genitalia, and also resembles *Caenaugochlora*, especially in the marginal cell, and epistomal sulcus. Neither phenogram places *Andinaugochlora* close to *Neocorynura*. The distance matrix places *Andinaugochlora* nearest to *Augochlorella* (9.896) and the correlation matrix to *Halictillus* (9.262), neither of which is very closely related cladistically to *Andinaugochlora* in my opinion. Until the Andean Halictinae are much more thoroughly collected and studied, the cladistic relationships of *Andinaugochlora* will remain in doubt.

Species of *Paroxystoglossa* occur on the southern margins of the range of *Neocorynura* and most females in particular are very similar to species of that genus. The correlation phenogram clusters *Paroxystoglossa* and *Neocorynura* together, although the distance phenogram does not, and the distance matrix places *Paroxystoglossa* nearest to *Augochlorella* (9.928).

Neocorynura resembles *Corynura* in the galeal comb and to some extent in genitalic characters. Early workers usually synonymized *Neocorynura* and *Corynura* on account of the long petiolate metasoma of the male, common to both. Both phenograms suggest a similarity of the *Corynura* group to *Neocorynura*. Outside its group the greatest similarity to *Neocorynura s. s.* in the correlation matrix and next closest in the distance matrix is with *Corynura*.

AUGOCHLOROPSIS GROUP. The large widespread genus *Augochloropsis s. l.* and the small southern Brazilian genus *Augochlorodes* form a small group not obviously related cladistically to any other group, and phenetically distinct as indicated by the low clustering level of *Augochloropsis* on both phenograms. The correlation matrix and phenogram would suggest a similarity of *Augochloropsis* to *Temnosoma* at a low level (0.174), but there is little reason to suggest a close cladistic relationship. The distance matrix places *Augochloropsis* nearest to *Thectochlora* at a low level of similarity (1.185). The very close similarity between *Augochloropsis s. s.* and *Paraugochloropsis* suggested by the phenograms may in part be due to the difficulties in coding genitalic characters.

Augochlorodes is placed in a group with *Augochloropsis* on the basis of the structure of its head and mouthparts and male sternal and genital characteristics, although *Augochlorodes* lacks most of the other distinctive characteristics of *Augochloropsis*. Neither of the phenograms clusters *Augochlorodes* closely with any other genus; both matrices place *Augochlorodes* as very slightly more similar to *Andinaugochlora* than to other genera. Neither matrix indicates a particularly close similarity to *Augochloropsis*.

THECTOCHLORA. This is a small genus from the southern Brazilian and Argentinian region which could not be cladistically linked to other genera. While *Thectochlora* is clustered ambivalently in the phenograms, both matrices place it as most similar to *Ceratalictus* (0.861 distance, 0.271 correlation). This is not necessarily an indication of cladistic relationship, in my opinion.

AUGOCHLORA GROUP. *Augochlora, Oxystoglossella, Mycterochlora, Augochlorella, Ceratalictus,* and *Pereirapis* form a cohesive widespread group. Vachal (1911) had recognized the *Augochlora* group as the *Halicti falcati*, and it largely corresponds with Moure's (1943) original Augochlorini. The group is united phenetically by such characters as a common tibial spur form and basic genitalic structure. The correlation phenogram also reflects my concepts concerning the cladistic relationships within the group, with *Mycterochlora* being less similar and less related cladistically to *Augochlora*

s. s. than is *Oxystoglossella*, and *Ceratalictus* being very similar and closely related cladistically to *Augochlorella*. The distance phenogram separates *Augochlora s. l.* from the other members of the group, but this appears to be misleading, as in the matrix, *Oxystoglossella* shows the highest similarity outside its genus to *Augochlorella* (0.989), as does *Augochlora s. s.* (1.004). The cladistic relationships of the *Augochlora* group to other groups are obscure; *Ceratalictus* with its obtuse epistomal sulcus, short glossa, lack of unique features found in other genera of the group, and southern range, may prove to be the most primitive and an important connecting link, perhaps to *Paroxystoglossa*. Both matrices suggest that *Ceratalictus* is most similar to *Thectochlora* outside its group.

PSEUDAUGOCHLOROPSIS GROUP. *Pseudaugochloropsis*, *Caenaugochlora*, and *Ctenaugochlora* form a loosely knit group of bees with long glossae and characteristically modified metasomal sterna IV of the males. *Caenaugochlora s. l.* is characterized by such interesting features as spiculum-like anterior apodemes on metasomal sterna VI and VII of the males and long hair on the eyes. Despite the fact that some females of *Caenaugochlora s. l.* can be separated from *Pseudaugochloropsis* only with difficulty and the mouthparts are usually quite similar, neither the phenograms nor matrices indicate strong similarity between the two. Both *Caenaugochlora* and *Pseudaugochloropsis* are clustered with different genera at low levels in the two numerical analyses. The form of the mouthparts and epistomal sulci suggest a possible cladistic relationship with the *Megaloptidia* group.

MEGALOPTA. This genus exhibits such a variety of unusual characteristics, including the continuous row of hamuli, female labral structure, pronotal structure, and male genitalia, that it could not be placed with certainty in any group. The structure of the mouthparts, characteristics of the male sterna, and long marginal cell (as in *Caenaugochlora*) suggest a possible cladistic relationship with the *Pseudaugochloropsis* group. The enlarged eyes and ocelli and general appearance also are similar to those of members of the *Megaloptidia* group, as shown in the correlation phenogram. In the correlation matrix, *Megalopta* is closest to *Pseudaugochloropsis*, although at a low level of similarity (0.113). The distance phenogram shows *Megalopta* to be one of the most distinctive of the genera; the matrix indicates no closely similar genera. Examination of the males of the small-eyed species of *Megalopta* may give further clues as to the genera which may be most closely related cladistically to it.

MEGALOPTIDIA GROUP. *Megommation*, *Megaloptina*, *Megaloptidia* and *Ariphanarthra* form a closely knit group of rather shiny bees characterized in particular by their unique, long, slender mouthparts. The scarceness of males in collections hampered analysis of cladistic relationships within the group. Both phenograms clearly distinguish the group and portray com-

parable intragroup similarities, reflecting my ideas of cladistic relationship. The *Megaloptidia* group appears to be most closely related cladistically to the *Pseudaugochloropsis* group, and its similarity to the latter is suggested by both phenograms and the correlation matrix; both *Megommation s. l.* and *Ariphanarthra* have their highest correlations outside their group with *Pseudaugochloropsis,* although at low levels, 0.194 *(Megaloptina)* and 0.160 *(Ariphanarthra).*

CHLEROGELLA. This genus cannot as yet be placed into a group, as it is known from a single female and is unusual in several respects, notably the elongate head and the pronotal structure. The phenetic clustering of *Chlerogella* with *Chlerogas* is quite probably artificial and does not reflect cladistic relationship, as both are known only from one sex (in *Chlerogas,* the male) and both have elongate heads. In general appearance, color, and the long marginal cell, *Chlerogella* somewhat resembles *Corynurella,* to which it is most similar in the distance matrix (1.381) and second most similar (following *Chlerogas*) in the correlation matrix (0.277); whether this indicates a cladistic relationship is uncertain.

TEMNOSOMIA. This genus appears to be the most distinctive genus, and this is confirmed by the distance phenogram. The correlation matrix suggests a similarity to *Augochloropsis,* although the correlation is low (0.179 with *Augochloropsis s. s.*), but the matrix shows that correlations are negative or nearly so with all other genera. A cladistic relationship with *Augochloropsis* is not suggested by most characters in this study, although *Augochloropsis* does contain some coarsely punctate species which suggest a resemblance to *Temnosoma,* unlike most other genera.

Phylogenetic speculations: Cladistic analysis and the construction of "phylogenetic trees" requires that the primitive and advanced states of characters be ascertained. While such decisions are speculative for the Augochlorini, they are of heuristic value; therefore, Table 1 lists for certain characters the probable primitive and advanced states, based on comparisons with other bees outside the Augochlorini, sometimes outside the Halictinae.

Using the characters in this table, it is possible to speculate further on which genera are primitive and on lines of evolution. The *Corynura* group appears to be the most primitive group, as particularly indicated by the well-developed galeal comb; short, wide mouthparts; and usually non-brilliant coloring. If the *Corynura* group is accepted as a base for evolution, then the *Rhinocorynura* group is closely related cladistically, sharing many of the primitive characters. Both the *Corynura* and *Rhinocorynura* groups occupy ranges in temperate and subtropical South America.

The *Neocorynura* group appears to be an evolutionary offshoot of the *Corynura* group that has successfully radiated in the tropics and undergone a great amount of speciation. Many of the specializations of *Neocorynura*

Table 1. Primitive *vs* Specialized Features of Augochlorine Genera.*

Character	Primitive	Specialized
angle of epistomal sulcus	obtuse	acute
clypeus	normal	flattened, protuberant, or projecting beyond margin
clypeal modifications	normal	tuberculate or spined
malar area	normal	elongate
preoccipital ridge	rounded	carinate
hypostoma	short and wide	long and narrow
emargination of compound eye	shallow	deep
eye hair	normal	long
ocelli	normal	enlarged
mandibular tooth	normal	absent or enlarged
maxillary anterior conjunctival thickenings	joining distally	normal
apex of galea	normal (lobed)	pointed
galeal comb	present	absent
maxillary palpus	normal	greatly elongate
prementum (anterior surface)	normal	transparent or without premental thickenings
prementum	short and wide	long and narrow
glossa	short	long
mesoscutum	normal	narrowed anteriorly
tegula	normal	modified
distal hamuli	single row	normal
inner hind tibial spur	serrate or pectinate	rounded-serrate or lamellate
scopa	present	absent
basitibial plate	long, all edges defined	short, or all edges not defined, or absent
pseudopygidial area	normal	scaled or absent
sternum I	normal	spined or tuberculate
antenna (male)	normal	hooked or with projections
inner hind tibial spur (male)	normal	knobbed or pectinate
metasoma (male)	oval or elongate	petiolate
sterna III-VI	normal	modified
basal process of ventral gonostylus	present	absent
color	black or dull metallic	bright green or testaceous (orange)

* Normal states are explained in the section on Characters Employed.

heighten the resemblance of these bees to polybiine wasps, which are common in many of the habitats where these bees are found. The question immediately arises whether mimicry is involved, and if the apparent evolutionary success of *Neocorynura* is in part due to it. In most respects species of *Neocorynura* are quite generalized, especially in the mouthparts and the presence of a rudimentary galeal comb.

Augochloropsis is a highly successful product of augochlorine evolution that has spread through most of the tropics and the North Temperate Zone

of the New World. Although the mouthparts of most species are not obviously specialized, many species seem to be adept at gathering pollen from plants in predominantly tropical families (such as Solanaceae and Melastomaceae, as observed in Costa Rica) which require behavioral adaptations on the part of the bees, and this may in part account for the success of the genus. *Augochlorodes* may represent a cladistically more primitive member of the group, but I could not determine from which generic group it might have descended.

Augochlora is also a successful and widespread genus, with an elongate glossa and modifications for wood dwelling in species of the principal subgenus. *Augochlora* is the end of a cladistic line whose most primitive member, *Ceratalictus,* is in the Southern Hemisphere. *Augochlorella,* less specialized than *Augochlora,* is most numerous in species in temperate North America, less so in the tropics.

The *Pseudaugochloropsis* group appears to represent still another line of evolution, possibly related cladistically to some member of the *Neocorynura* group. The former may be important as a cladistic link to *Megalopta* and the *Megaloptidia* group. *Megalopta* is one of the most specialized genera; many of the modifications of its species apparently are linked to nocturnal habits and wood dwelling. The *Megaloptidia* group also represents a distinctive evolutionary line; the highly modified mouthparts, enlarged eyes and ocelli in some species, and the rareness of specimens in collections despite a wide range of the genera, suggest behavorial specialization.

Temnosoma is apparently the only augochlorine genus whose species are social parasites, judging from the morphology of the adult bees. Phenetically it is the most distinct of the augochlorine genera and its cladistic relationships could not be ascertained. The thick, very coarsely punctate integument and general chrysidid-like appearance of its species suggest that they are even better adapted morphologically to social parasitism than are species of the well known and widespread genus *Sphecodes.*

The above phylogenetic scheme postulates that the most primitive augochlorines (the *Corynura* group) are presently South Temperate in distribution and that the more specialized and cladistically more recent genera are principally tropical. The range of *Corynura,* interestingly, coincides to some extent with the range in America of the most primitive bees, the Paracolletini (Colletidae) (Michener, 1944). It is quite possible, of course, that a member of the *Neocorynura* group was the most primitive and that the *Corynura* group has evolved from it.

The four well-defined generic groups and the other genera are quite distinctly set apart from each other. This is especially apparent when the male genitalia are considered; distinct structural patterns are evident within the genitalia of many genera that are not easily homologized with patterns of

other genera. This is in contrast to most non-augochlorine genera of American halictine bees where the genera are poorly separated and the genitalia follow the same basic structural plan (Eickwort, in preparation). The speculation arises as to whether this indicates that the Augochlorini are the older group of Halictinae in the Americas, having more thoroughly differentiated into supraspecific taxa.

Geographic distribution: Discussion of geographical distribution is severely hampered by the paucity of specimens available from northern and western South America. This is especially evident for the Andes, where comparatively few species have been collected. Unique specimens from the Andes suggest an abundance of new genera, new radiations of previously known genera, and possible links that will help clarify cladistic generic interrelationships. The United States, Mexico, Costa Rica and Panamá, Southern Brazil, Argentina, and Chile have been comparatively well collected for augochlorine bees. Even in these countries, "rare" bees are occasionally encountered that represent new genera. For instance, the single female of *Chlerogella* collected by Michener in Panamá is very different from genera previously known. Moure (1951) has described a similar case in his efforts to obtain specimens of *Ariphanarthra palpalis* in a well-collected area of southern Brazil.

North American halictines are largely polylectic and visit a variety of weedy herbs, and many Latin American halictines follow this pattern, e.g., many *Augochlora* (*Oxystoglossella*) and *Pereirapis*. But many, and perhaps most, tropical American augochlorine bees appear to be more specific in flower visitation and habitat selection, and this may lead to their being poorly collected, even by experienced collectors in the right geographical locations. For instance, *Megalopta* is a widespread genus of large nocturnal bees, but they are well represented in collections only because they are attracted to lights at night. Specimens collected in daytime are rare.

Eight genera are considered widespread in distribution, ranging from North America or Mexico to Argentina: *Augochlora*, *Augochloropsis*, *Augochlorella*, *Pereirapis*, *Pseudaugochloropsis*, *Megalopta*, *Temnosoma*, and *Neocorynura*. *Caenaugochlora* and *Megommation* are nearly as widespread, occurring in both Central and South America.

South America north of Argentina and Chile is the center of abundance of augochlorine genera; besides the above-named widespread genera, *Andinaugochlora*, *Chlerogas*, *Rhinocorynura*, *Halictillus*, *Corynurella*, *Rhectomia*, *Paroxystoglossa*, *Augochlorodes*, *Thectochlora*, *Ceratalictus*, *Megaloptidia*, and *Ariphanarthra* are known from this region. The last ten genera occur from southern Brazil to northern Argentina and may indicate that this region is an important center of diversification, or knowledge of them there may

simply be a result of the intensive collecting in that region and subsequent systematic studies.

The *Corynura* group is the most important component of the fauna of Chile (Moure, 1964); other augochlorine genera (i.e., *Temnosoma*) are rarely collected in the northern region of the country. This group is also conspicuous in the fauna of Argentina, although most of the genera known from southern Brazil are also represented in collections from that country.

While Central America and Mexico are rich in species of the widespread augochlorine genera, only one genus, *Chlerogella,* is known exclusively from this area. The Caribbean region, excluding Trinidad and Cuba, is not well collected. As pointed out by Cockerell (1910), Trinidad should not be included in a discussion of this region, as its faunal connections are with Venezuela. There are no unique augochlorine genera known from the Caribbean; *Augochlora, Pseudaugochloropsis, Neocorynura,* and *Temnosoma* are the only genera I have seen represented from islands other than Trinidad.

Only the northernmost species of five widespread, principally tropical, genera are known from the United States and Canada: *Augochlora, Augochlorella, Augochloropsis, Temnosoma,* and *Pseudaugochloropsis* (Ordway, 1966). The latter two genera are known in the United States only from southern Arizona and southern Texas, respectively.

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APPENDIX 1. DESCRIPTIONS OF NEW SPECIES AND LECTOTYPE DESIGNATION

Corynurella mourei, new species

(Figs. 117, 184, 282, 335, 336)

Female. Length, 6.5 mm; wing length, 5 mm. Head about as wide as long, wider than mesosoma. Vertex produced above ocelli; gena about as wide as eye in lateral view. Clypeus and supraclypeal area slightly protuberant, each gently rounded, supraclypeal area below antennae longer than clypeus; clypeus projecting about half its length below lower margins of eyes. Frontal line weakly carinate, continued as impressed line to median ocellus. Lateral ocelli much nearer each other than to compound eyes; joined above by weakly impressed line. Compound eyes weakly emarginate, converging more below than above. Proboscidial fossa rather long, hypostomal l/w = 1.83; hypostomal bridge suture "open" nearly to posterior margin; c/l = .17; hypostomal carina not produced, anterior angle rounded; hypostoma widest near posterior flange; posterior flange rounded, slightly protruding beyond margin of occiput. Preoccipital ridge completely rounded; postgenal bridge suture "open" for about ¾ of its length. Measurements of head of holotype in mm: width, 1.72; length, 1.91; clypeal length, .385; lower interorbital distance, .78; upper interorbital distance, .98; clypeo-antennal distance, .41; interantennal distance, .15; antennocular distance, .30; antennocellar distance, .52; interocellar distance, .21; ocellocular distance, .29. Scape reaching to upper margin of median ocellus, length, .71; pedicel longer than wide, length .15; flagellomere 1 longer than wide, length .12; flagellomeres 2 and 3 wider than long, subequal, shorter than 1, length 2, .11; 3, .10; 4 about as long as wide, length, .14; flagellomeres then slightly increasing in length distally; 10 slightly longer than wide, length, .16; terminal flagellomere length, .30. Labrum with distal process medially narrow, expanded basally as two rounded lobes with fimbria on surface; labral teeth poorly defined distally, absent basally; distal keel normal, not flattened. Mouthparts p/M = .45, pw/pl = .17, pl/W = .87, gl/pl = .57, gl/W = .50; galeal comb of 9 or 10 teeth in specimen dissected. Median and parapsidal lines of mesoscutum weakly impressed. Median scutellar impression not evident. Basal area of propodeum slightly longer than scutellum and over twice as long as metanotum; propodeal triangle weakly impressed; lateral carinae of posterior surface of propodeum short, barely surpassing posterior submarginal

pits. Marginal cell of forewing extending nearly to apex of wing, mc/wl = .79. Submarginal cells 2 plus 3 subequal in length to 1 on lower margin; 2 not greatly narrowed anteriorly; cells 2 and 3 both receive a recurrent vein. Stigma very large. 1/w = 2.30. About 5 hamuli (arranged 2-1-2) on hind wing. Front trochanter rather long and narrow, about 3 times longer than wide. Hind femur with lower surface slightly concave; scopa not dense. Basitibial plate well defined but rim not raised above surface of plate; plate smooth but not glossy; no setae on plate. Inner hind tibial spur with about 4 rounded teeth, decreasing in length apically. Pseudopygidial area of metasomal tergum V transparent, with few long setae.

Integument rather shiny and weakly punctured. Face closely but weakly and obscurely punctured, punctures less distinct below antennal sockets; supraclypeal area and clypeus polished; with scattered obscure punctures of medium depth, vertex polished, not punctate; gena shiny but obscurely roughened; postgena with close fine obscure longitudinal roughening, not shiny. Anterior surface of pronotum polished; lateral surface with poorly defined striae parallel to lateral ridge. Mesoscutum and scutellum polished, not punctured; metanotum with no evident punctures, slightly less polished. Mesepisternum and metepisternum polished, not punctured; pre-episternum shiny but slightly obscurely roughened; ventral surface of mesepisternum obscurely roughened. Basal area of propodeum shiny, with fine, close concentric striae not interrupted medially, anterior striae bow-shaped, posterior striae transverse; striae not reaching slightly raised polished rim of basal area; lateral and posterior surfaces polished, not punctured. Dorsum of metasoma shiny, punctures not evident, anterior surface of tergum I polished; venter of metasoma with obscure punctures bearing setae, less shiny.

Color generally testaceous, head and mesosoma largely suffused with dark metallic blue-green. Head blue-green; edge of clypeus, labrum and mandibles (except red-brown tips) testaceous. Scape yellow, clouded with brown on inner surface near apex; pedicel and flagellum dark brown, lighter beneath. Mesosoma blue-green, testaceous undertones more evident on pleura and venter; pronotal lobe testaceous; tegula yellowish-hyaline; wing membrane clear; veins and stigma brown; legs yellowish-testaceous; upper surface of hind tibia slightly infuscated. Metasomal segments I to III testaceous; rest of metasoma dark brown; extent of brown pigmentation variable, sometimes darkening most of segments II and III.

Pubescence of head sparse, pale; gena behind eye and parocular area from epistomal lobe to notch of eye with short, appressed, distinctly plumose, white setae, not obscuring surface. Pubescence of dorsum of mesosoma pale, not dense nor obscuring surface, setae longest on scutellum and metanotum, absent or basal area of propodeum; dense fringe of white setae covering first thoracic spiracle, on edge of pronotal lobe; pubescence of mesepisternum white, densest on venter and near pre-episternal sulcus, not obscuring surface; pubescence on lateral and posterior surfaces of propodeum pale, long, weakly plumose, not dense. Leg setae pale to testaceous, more reddish on tibiae and tarsi, not dense or especially long. Pubescence of dorsum of metasoma pale, sparse, not appressed, long and erect on anterior surface of tergum I; fimbria of terga V and VI denser, golden; postgradular areas of sterna with long erect pale setae distally.

Male. Length, about 7 mm; wing length, 4.5 mm. Head longer than wide, about as wide as mesosoma; gena narrower than eye in lateral view; supraclypeal area below antennae slightly shorter than clypeus; eyes slightly more deeply emarginate than in female, converging more strongly below; frontal line more weakly defined; median impressed line to median ocellus very weakly defined; line not impressed behind lateral ocelli. Measurements of head of allotype in mm: width, 1.47; length, 1.76; clypeal length, .43; lower interorbital distance, .54; upper interorbital distance, .83; clypeo-antennal distance, .36; interantennal distance, .17; antennocular distance, .21; antennocellar distance, .50; interocellar distance, .18; ocellocular distance, .26. Agrees with description of female except for usual sexual differences and as follows: scape slightly shorter, length, .51; pedicel shorter, about as wide as long, length, .15; flagellomere 1 slightly longer than wide, length, .15; 2 subequal in length to 1 but shorter than 3, length, .15; 3 length, .20; flagellomeres slightly increasing in length distally, 10 about 2/3 as wide as long, length, .22; terminal flagellomere length, .30. Distal process of labrum hidden by mandibles; basal area with prominent setae below bevel of basal elevation. Metasoma rather narrow and elongate; sterna VII and VIII illustrated in Fig. 282; genitalia illustrated in Figs. 335 and 336.

Punctation generally weaker than in female; postgenal roughening not defined, shiny; lateral surface of pronotum without striae; basal area of propodeum with striae more weakly defined, only extending about half the length of propodeum along midline, rim of basal area glossy, wide.

Color more yellowish-testaceous; dark blue-green tints generally less intense; lower half of clypeus, labrum, and mandibles (except reddish tip) yellow-testaceous; scape translucent-yellowish, dusky distally; metasomal terga V and VI partly testaceous, brown pigmentation of metasoma not as dark. Pubescence generally similar to that of female except for usual sexual differences.

Type material. Holotype female, allotype male, and 2 paratype females, Brasil, Rio de Janeiro, Baia de Guanabara, Floresta dos Macacos, April 1961 (M. Alvarenga); 3 paratype females, same data, 16 February 1961; 2 paratype females, Floresta de Tijuca, Brasil, 23 February 1953, C. A. C. Seabra coll.; 1 paratype female, same data, 7 February 1953. Holotype and allotype in the Snow Entomological Museum of The University of Kansas; paratype females in that collection, the collection of Pe. J. S. Moure (Universidade do Paraná, Brasil), and the collection of Dr. C. A. C. Seabra (Rio de Janeiro, Brasil).

This species is named in honor of Pe. J. S. Moure, C. M. F., of the Universidade do Paraná, Brasil, in recognition of the aid he has given me in this study and of the contributions he has made to the study of South American bees.

Corynurella mourei is readily distinguished by its largely testaceous coloration, elongate marginal cell and large stigma of the forewings, and unusual pronotal structure. A macrocephalic female of this or a closely-related species from Yurac, 67 mi. E. of Tingo Maria, Peru, 11 December 1954, E. I. Schlinger and E. S. Ross, colls., is in the collection of the California Academy of Sciences, San Francisco.

Andinaugochlora micheneri, new species

(Figs. 121, 148, 203, 212, 241, 290-292, 358-361)

Female. Length, 9.0 to 9.5 mm; wing length 7.5 mm. Head wider than long, about as wide as mesosoma; gena about as wide as eye in lateral view. Supraclypeal area protuberant, rather abruptly beveled; clypeus protuberant and rounded; clypeus and supraclypeal area below antennae subequal in length; clypeus projecting over half its length below lower margins of eyes. Frontal line weakly carinate, not extending as impressed line to median ocellus; no impressed line behind lateral ocelli. Compound eyes strongly emarginate, converging about equally below and above. Proboscidial fossa rather long, hypostomal l/w = 1.49; hypostomal bridge suture closed about half its length, c/l = .43; hypostomal carina not produced, anterior angle rounded; fossa widest near posterior flange; posterior flange truncate, projecting beyond margin of occiput. Preoccipital ridge weakly carinate laterally and dorsally, not carinate near junction with hypostomal carina; postgenal bridge suture open for about half of its length. Measurements of head of holotype in mm: width, 2.63; length, 2.30; clypeal length, .59; lower interorbital distance, 1.38; upper interorbital distance, 1.49; clypeo-antennal distance, .50; interantennal distance, .25; antennocular distance, .58; antennocellar distance, .70; interocellar distance, .30; ocellocular distance, .28. Scape reaching to level of top of lateral ocelli, length, 1.10; pedicel slightly longer than wide, length, .20; flagellomere 1 subequal to pedicel, longer than wide, length, .20; 2 wider than long, length, .15; 3 as long as wide, length, .17; flagellomeres slightly increasing in length distally, 10 about as long as wide, length, .23; length terminal flagellomere, .34. Labrum illustrated in Fig. 148. Mouthparts p/M = .33; pl/W = .70; pw/pl = .18, gl/pl = .52; gl/W = .36; galeal comb of 3 to 5 short teeth. Mesoscutal lip rather high and narrow, but rounded and not strongly projecting over pronotum; median line and parapsidal lines moderately impressed. Scutellum not impressed medially; basal area of propodeum subequal in length to metanotum; metanotum about two-thirds as long as scutellum; propodeal triangle clearly indicated; lateral carinae of posterior surface of propodeum diverging, extending slightly less than halfway to basal area. Submarginal cells 2 plus 3 of forewing subequal in length to 1; 2 rather narrow and receiving first recurrent near apex or interstitial with 2nd transverse cubital; about 8 hamuli (arranged

4-1-3) on hind wing. Hind femur not concave on lower surface, scopa moderately dense; inner hind tibial spur with about 3 teeth (Fig. 212); basitibial plate as in Fig. 203.

Integument not at all shiny; face above antennal sockets and vertex closely and densely punctate, punctures contiguous; parocular area below antennae with obscure punctures, surface finely granular; supraclypeal area above level with rather close and obscure punctures; below bevel and upper portion of clypeus with finely granular surface and weak, widely spaced punctures, not shiny; clypeus below bevel not granular, with coarser obscure punctures. Gena obscurely roughened above, finely and closely striate below, behind lower portion of eye; postgena very finely granular, not shiny or striate. Dorsal surface of pronotum directly behind pronotal lip smooth, polished bordering mesoscutal lip, pronotum otherwise smooth or obscurely roughened and not shiny. Mesoscutal punctures distinct but rather fine, slightly smaller than punctures on vertex, contiguous over most of mesoscutum, somewhat obscure near anterior-lateral angles, slightly more separated in central area of mesoscutum, there rarely separated by more than their diameter. Scutellar punctures slightly coarser, not contiguous but separated by less than their diameter; metanotal punctures fine and close, not well defined. Pre-episternum obscurely roughened, slightly shiny; mesepisternum and upper portion of metepisternum transversely striate; ventral surface of mesepisternum obscurely roughened, lower portion of metepisternum finely granular. Basal area of propodeum finely granular, with light obscure basal striations, not reaching posterior margin; lateral and posterior surfaces obscurely roughened or finely granular. Dorsum of metasoma smooth or slightly roughened but not shiny, basal zones of terga and anterior surface of tergum I with fine close punctures or lightly and obscurely roughened; posterior marginal areas depressed and smooth. Venter with punctures bearing setae; posterior marginal areas depressed and smooth.

Integument green with cupreous areas, these areas occasionally partially yellowish or green. Face cupreous with vertex and frons greenish; gena and postgena green with golden or cupreous tints; apical half of clypeus, labrum, and mandible (except red-brown tip) dark brown; scape and upper surface of flagellum dark brown; lower surface of flagellum ferruginous. Central area of mesoscutum, between parapsidal lines, cupreous, color sharply delimited from green to cupreous-green of remainder of mesosoma; shiny dorsal surface of pronotum cupreous. Tegulae dark brown, anterior outer edge hyaline, anterior inner edge green; wing slightly infuscated, veins and stigma medium brown; vein R dark brown. Coxae, trochanters, femora, front tibiae dark brown with green tints, rest of legs fuscous. Dorsum of metasoma, including posterior marginal areas, green, often slightly yellowish or purplish; extreme posterior edges of terga brownish; venter dull brownish-green; posterior marginal areas and sternum VI brown.

Pubescence of head long, plumose, and erect; on face pale with some dark setae interspersed; on frons and vertex, dark; on genae and post-genae, pale. Mesoscutum with very short dense pubescence, obscuring most of surface, few longer setae intermixed; most of central cupreous area overlaid with dark brown pubescence, contrasting strongly with white lateral pubescence; zone of white pubescence extending narrowly across posterior margin of mesoscutum; setae longer and yellowish on anterior-lateral angle of mesoscutum; scutellum with similar dense, short, dark brown pubescence, laterally with some longer pale setae; metanotum with short, dense, white pubescence, longer golden setae intermixed; laterally with longer pale setae. Dorsal surface of pronotum behind pronotal lip with dense, short, pale setae; pronotum otherwise with scattered pale setae; first thoracic spiracle covered by dense fringe of white setae, on edge of pronotal lobe. Mesepisternum laterally and metepisternum bare, scattered pale setae on venter of mesepisternum. Basal area of propodeum bare; upper edge of lateral surface with zone of rather thick pale plumose setae of moderate length; lateral surface with very short fine setae and scattered long setae; posterior surface with moderately long, plumose, erect setae. Pubescence of coxae, trochanters, and femora pale, long on ventral surface of front femur; mesofemoral brush golden; pale yellowish hairs on ventral surfaces of tibiae, brown on dorsal surfaces, pubescence dense on hind tibia and apex of dorsal surface of middle tibia; mesotibial comb golden; pubescence of anterior surfaces of basitarsi brown, of posterior surfaces golden; of remainder of tarsi ferruginous; penicillus ferruginous. Pubescence of anterior surface of metasomal tergum I pale, erect, moderately long; of dorsal

surface of tergum I and terga II to IV very short, pale, inconspicuous, slightly longer laterally; prepygidial and pygidial fimbria fuscous-ferruginous; pubescence of venter moderately long and dense, pale, weakly plumose; on sternum V somewhat yellowish; slightly ferruginous on VI.

Male. Length, about 9 mm; wing length, 7.5 mm. Head about as wide as long, about as wide as mesosoma; clypeus much longer than supraclypeal area below antennae; eyes more deeply emarginate than in female, converging more strongly below. Hypostomal bridge suture closed just at flange. Measurements of head of allotype in mm: width, 2.36; length, 2.24; clypeal length, .59; lower interorbital distance, .99; upper interorbital distance, 1.38; clypeoantennal distance, .37; interantennal distance, .36; antennocular distance, .35; antennocellar distance, .62; interocellar distance, .28; ocellocular distance, .28. Agrees with description of female except for usual sexual differences and as follows: antenna very long, surpassing propodeum; scape shorter, not reaching median ocellus, length, .63; pedicel about as wide as long, length, .14; flagellomere 1 length, .17; flagellomere 2 much longer than 1, longer than wide, length, .33; flagellomeres increasing in length apically, length 3, .37; length 10, .47; terminal flagellomere length, .57; plate areas present. Metasoma narrow and elongate, sterna IV and V with posterior margins slightly concave medially, central areas slightly depressed; sternum VI as in Fig. 241; hidden sterna and genitalia as illustrated in Figs. 290-292, 358-361.

Gena not striate; postgena obscurely roughened. Scutellar punctures more widely spaced than in female, frequently more than a diameter apart, closer along midline and near edges; scutellum somewhat shiny; mesepisternum and metepisternum obscurely roughened or with very obscure punctures, somewhat shiny near middle coxa; no striae except near top of metepisternum, where poorly defined. Basal area of propodeum slightly shiny at posterior margin; posterior and lateral surfaces of propodeum with obscurely defined punctures or obscurely roughened.

Integument without cupreous areas; head green with yellowish tints; postgena near anterior angle of hypostomal carina dark purplish-brown; clypeus entirely green except for posterior margin, margin of clypeus, labrum and mandible (except reddish tip) dark brown. Scape green; pedicel and upper surface of flagellum dark brown; lower surface yellowish, color sharply delimited posteriorly. Mesosoma green with yellowish tints; legs green except dark brown tarsi. Metasoma dorsally blue-green, with violet highlights; extreme posterior edges of terga brownish.

Pubescence of head longer than in female; mesosoma without areas of short dense pubescence; pubescence of dorsum long, plumose, not dense, brown medially and pale laterally; mesepisternum with rather long, pale brownish, plumose pubescence. Pubescence of legs much sparser, generally paler. Tergal pubescence pale and sparse, but longer and more evident than that of female.

Type material. All from Ecuador. Holotype female, allotype male, and 37 female, 44 male paratypes, Oriente-Ambato, 2600 m, October 1956; 1 paratype male, same data, December 1956; 2 paratype females, Cotocallao, October 1950; 1 paratype female, Cotocallao, Pichincha Prov., 27 April 1958, 10,000 ft. elev., R. W. Hodges, coll.; 8 paratype females, Quito, Pichincha, 15 January 1958, R. W. Hodges, coll.; 1 paratype female, 5 mi. S of Latacunga, Cotopaxi, 2800 m, 7 February 1955, E. I. Schlinger and E. S. Ross, colls.; 1 paratype male, 7 mi. S Cayambe, Pichincha, 2740 m, 27 February 1955, E. I. Schlinger and E. S. Ross, colls. Holotype and allotype in the Snow Entomological Museum of The University of Kansas, paratypes in that collection, the Michigan State University entomological museum, the California Academy of Science, the United States National Museum, and the collection of Pe. J. S. Moure (Universidade do Paraná, Brasil).

This species is named in honor of Dr. C. D. Michener of The University of Kansas, in recognition of the guidance given me throughout this study and of the contributions he has made to the study of halictine systematics and biology.

The female of *Andinaugochlora micheneri* can be distinguished from related undescribed species by the unusual dorsal pattern of pubescence and coloration of the mesosoma and the striate bare episterna. The males can be distinguished from *Neocorynura* by the modifications of the sixth metasomal sternum and from related species by the bluish metasoma, green head and mesosoma, and dark tarsi.

Augochloropsis (Paraugochloropsis) metallica (Strand)

NEW COMBINATION, preoccupied. [Probable junior synonym of *Augochloropsis argentina* (Friese)]

Rivalista metallica Strand, 1921. Arch. Naturgeschichte, Abt. A, 87:270. (Preoccupied in *Augochloropsis* by *metallica* (Fabricius), 1793, Entomologia Systematica 2:209.7, published as *Andrena metallica*.)

With the kind help of Dr. J. Ochlke, I have been able to examine the two male cotypes of *Rivalista metallica* Strand from the Deutsches Entomologisches Institut (Eberswalde, East Germany) and place that species in *Augochloropsis (Paraugochloropsis)*. As neither Strand (1921) nor Bluthgen (1928) designated which specimen was to be considered the holotype of *metallica*, I hereby designate the specimen labeled "Usambara, A. Heyne, Berlin-Wilm., coll. Kraatz, Rivalisia metallica m., Strand det., paratypus," as hololectotype and have so labeled it. The genitalia of this specimen had been dissected and glued to a paper triangle pinned with the specimen. The second specimen, similarly labeled except that "typus" replaces "paratypus" is hereby designated a paralectotype and is so labeled. While Strand obviously had intended the latter specimen to be the type specimen of his species, its head is now missing, so I prefer to select the more nearly intact specimen. The genitalia of the paralectotype are not dissected.

In my opinion, the specimens are conspecific. They very closely resemble a specimen (which I have labeled as a homotype of *metallica* Strand) in the Snow Entomological Museum of The University of Kansas identified by Moure as *Augochloropsis argentina* (Friese), 1908, a common species in Argentina (Jensen-Haarup, 1908) and Brazil (Moure, 1944a). However, I prefer not to place *metallica* Strand into synonymy until types or homotypes of *argentina* and related species can be compared. I have no doubt that the specimens of *metallica* Strand are mislabeled as being from Africa and are in reality from South America, most likely from the region of southern Brazil to Argentina.

APPENDIX 2. ALPHABETICAL LIST OF GENERIC NAMES IN THE AUGOCHLORINI

Andinaugochlora n. g.
Ariphanarthra Moure
Augochlora Smith
Augochlorella Sandhouse
Augochlorodes Moure
Augochloropsis Cockerell

(*Cacosoma* Smith)=*Neocorynura (Neocorynura)* Schrottky
Caenaugochlora Michener
Callochlora Moure (subgenus of *Corynura* Spinola)
Ceratalictus Moure
Chlerogas Vachal
Chlerogella Michener
Corynura Spinola
Corynurella n. g.
(*Corynogaster* Sichel)=*Corynura (Corynura)* Spinola
(*Corynuroides* Sandhouse)=*Rhinocorynura* Schrottky
(*Corynuropsis* Cockerell)=*Rhinocorynura* Schrottky
Ctenaugochlora n. subg. (subgenus of *Caenaugochlora* Michener)
(*Ctenocorynura* Schrottky)=*Rhinocorynura* Schrottky

(*Glyptobasia* Moure)=*Augochloropsis (Paraugochloropsis)* Schrottky
(*Glyptobasis* Moure)=*Augochloropsis (Paraugochloropsis)* Schrottky
(*Glyptochlora* Moure)=*Augochloropsis ?(Paraugochloropsis)* Schrottky

Halictillus Moure

Megalopta Smith
(*Megaloptella* Schrottky)=*Megalopta* Smith
Megaloptidia Cockerell
Megaloptina n. subg. (subgenus of *Megommation* Moure)
Megommation Moure
(*Micraugochlora* Schrottky)=*Temnosoma* Smith
Mycterochlora n. subg. (subgenus of *Augochlora* Smith)

Neocorynura Schrottky
Neocorynuroides n. subg. (subgenus of *Neocorynura* Schrottky)

(*Odontochlora* Schrottky)=*Augochlora (Augochlora)* Smith
(*Oxystoglossa* Smith)=*Augochlora (Augochlora)* Smith
Oxystoglossella n. subg. (subgenus of *Augochlora* Smith)
(*Oxystoglossidia* Moure)=*Augochlorella* Sandhouse

(*Paraugochlora* Schrottky)=*Augochloropsis (Paraugochloropsis)* Schrottky
Paraugochloropsis Schrottky (subgenus of *Augochloropsis* Cockerell)
Paroxystoglossa Moure
Pereirapis Moure
(*Pseudaugochlora* Michener)=*Pseudaugochloropsis* Schrottky
Pseudaugochloropsis Schrottky

Rhectomia Moure
Rhinocorynura Schrottky
(*Rhopalictus* Sichel)=*Corynura (Corynura)* Spinola
(*Rivalisia* Strand)=*Augochloropsis (Paraugochloropsis)* Schrottky

Temnosoma Smith
(*Temnosomula* Ogloblin)=*Temnosoma* Smith
(*Tetrachlora* Schrottky)=*Augochloropsis (Paraugochloropsis)* Schrottky
Thectochlora Moure
(*Tmetocoelia* Moure)=*Megalopta* Smith

APPENDIX 3. PORTIONS OF NUMERICAL ANALYSIS OF AUGOCHLORINE GENERA

TABLE 2. Coding of character states for numerical analysis of augochlorine genera.

Character	States
angle of epistomal sulcus	(1) obtuse, (2) right, (3) acute
clypeus	(1) protuberant, (2) normally beveled, (3) flattened, (4) projecting beyond posterior margin
clypeal tooth	(1) normal, (2) prolonged
clypeal modifications	(1) normal, (2) tuberculate or spined
frontal line	(1) normal, (2) enlarged basally
malar area	(1) normal, (2) elongate
preoccipital ridge	(1) rounded, (2) rounded or sharply angled, (3) sharply angled or carinate, (4) carinate, (5) lamellate
vertex	(1) normal, (2) enlarged behind ocelli
hypostomal l/w	(1) over 1.75, (2) 1.50 to 1.75, (3) 1.00 to 1.50, (4) less than 1.00
hypostomal bridge suture c/l	(1) over .75, (2) .50 to .75, (3) less than .50
hypostomal carina	(1) normal, (2) posterior flange projecting
hypostomal carina	(1) normal, (2) anterior angle right angle or projecting
compound eye w/l	(1) less than .100, (2) .100 to .135, (3) over .135

Character	States
eye hair	(1) normal, (2) long
ocelli	(1) normal, (2) enlarged
labral distal process	(1) narrowly triangular, (2) broadly triangular, (3) expanded and narrowed apically, (4) expanded and rounded, (5) expanded and truncate
labral distal keel	(1) present, (2) absent
labral basal elevation	(1) oval, (2) orbicular, (3) transverse
labral basal elevation	(1) low, (2) strongly protuberant, rounded, (3) anterior surface flattened, (4) notched, (5) bituberculate
labral fimbria	(1) long, on margin, (2) short, on surface
mandibular tooth	(1) absent, (2) normal, (3) enlarged supplementary teeth may be present
mandibular width	(1) normal, (2) broadened
maxillary anterior conjunctival thickenings	(1) normal, (2) joining distally
apex of galea	(1) lobed (normal), (2) pointed
inner strip of galea	(1) broad markings, (2) narrow markings, (3) long setae on strip
galeal comb	(1) absent, (2) weakly formed, (3) well formed
maxillary palpus p/M	(1) less than .4, (2) over .4, (3) greatly elongate
prementum anterior surface	(1) transparent, (2) normal, (3) flattened, no premental thickenings
prementum width, pw/pl	(1) over .20, (2) .13 to .19, (3) .06 to .12, (4) less than .05
salivary plate	(1) normal, (2) normal or well-defined, (3) well-defined
glossal length, gl/W	(1) less than .25, (2) .25 to .40, (3) over .40
labial palpal segments 2 + 3	(1) longer than 1, (2) shorter than 1
pronotum dorsally	(1) concave, (2) convex
pronotal lateral angle	(1) rounded, nearly absent, (2) obtuse, (3) produced, acute or rounded, (4) carinate anteriorly, (5) produced above dorsal ridge
pronotal dorsal ridge	(1) rounded, (2) carinate or sharply angled, (3) lamellate
pronotal lateral ridge	(1) rounded, (2) rounded or sharply angled, (3) sharply angled, (4) sharply angled or carinate, (5) carinate, (6) lamellate
mesoscutum	(1) normal, (2) narrowed anteriorly
mesoscutal lip	(1) nearly absent, (2) rounded, (3) sharply angled and projecting forwards, (4) lamellate or carinate
tegula	(1) normal, (2) strongly pitted, (3) produced
basal area of propodeum	(1) smooth, (2) weakly striate or smooth, (3) striate
posterior surface of propodeum	(1) narrow, (2) normal, (3) broad
propodeal pit	(1) normal, (2) enclosed in notch
apex of marginal cell	(1) acute or narrowly truncate, (2) truncate and usually appendiculate
marginal cell mc/wl	(1) less than .65, (2) over .65
distal hamuli	(1) normal, (2) continuous row
inner hind tibial spur	(1) serrate, as in outer spur, (2) rounded serrations, (3) serrate to pectinate, (4) short-pectinate, (5) pectinate, (6) lamellate
scopa	(1) present, (2) absent
basitibial plate	(1) absent, (2) short, (3) normal
rim of basitibial plate	(1) raised rim, (2) normal, (3) obsolescent anteriorly
apex of basitibial plate	(1) broadly rounded, (2) narrowly rounded, (3) one edge defined only
anterior basitarsal brush	(1) weak or absent, (2) strong
pseudopygidial area	(1) absent, (2) normal, (3) scaled
tergum VI	(1) normal, (2) gradulus absent
sternum I	(1) normal, (2) spined or tuberculate
sterna IV-V	(1) resemble male, (2) with graduli, (3) without graduli

Character	States
antennal flagellomeres 2/1	(1) less than .85, (2) 1.00 to 1.50, (3) over 1.50
antennal length sc/2	(1) over 3, (2) 1 to 3, (3) less than 1
antennal modifications	(1) normal, (2) hooked, (3) projections on scape and pedicel
antennal plate areas	(1) absent, (2) present or absent, (3) present
labral distal process	(1) short or absent, (2) triangular, (3) expanded and rounded, (4) expanded and truncate
basal elevation of labrum	(1) extends across basal area, (2) notched, (3) not extending across basal area
inner hind tibial spur	(1) normal, (2) knobbed, (3) pectinate
patches of pubescence	(1) normal, (2) on propodeum, (3) on legs
metasoma	(1) petiolate, (2) elongate, (3) oval or elongate, (4) oval
tergum VII	(1) elongate, (2) gradually convex, (3) abruptly convex
gradulus of tergum VII	(1) absent or poorly defined, (2) present, well-defined
postanal filaments	(1) absent, (2) short or absent, (3) long
proctiger	(1) normal, (2) fringed with microtrichia
sternum III	(1) normal, (2) apex modified
sternum IV	(1) normal, (2) median setal clumps, (3) median tubercles or ridges
sternum IV	(1) normal, (2) lateral setal clumps, (3) lateral projections
posterior margin of sternum IV	(1) normal, (2) produced, (3) bilobed
sternum V	(1) normal, (2) median setal clumps, (3) median tubercles or ridges
sternum VI	(1) weakly notched, (2) strongly notched, (3) with depressions or median ridge, (4) flanged
apodemes of sternum VI	(1) normal, (2) narrow
posterior margin sternum VII	(1) membranous, (2) not produced, (3) median projection, (4) bilobed
sternum VII	(1) normal, (2) spiculum-like apodeme
posterior margin sternum VIII	(1) not produced, (2) median projection
junction sterna VII and VIII	(1) beyond apodemes, (2) at apodemes
spiculum of sternum VIII	(1) narrow, (2) broad
ventral bridge of gonobase	(1) membranous or narrow, (2) broad
dorsal lobes of gonobase	(1) slight, (2) strong and rounded, (3) strong and sharply angled
lateral ridge of ventral gonostylus	(1) not produced, (2) produced, (3) produced and lobed
lateral ridge of ventral gonostylus	(1) without setae, (2) with setae
basal process of ventral gonostylus	(1) present, (2) absent
parapenial lobe	(1) present, (2) absent
dorsal gonostylus	(1) absent or ridge, (2) membranous small area, (3) linear flap, (4) expanded shield
ventral gonostylus	(1) lobe narrowed basally, flattened surface with setae, (2) lobe produced from apex, (3) lobe broadly joining inner edge of gonocoxite
venter of penis valve	(1) ventral prong, (2) ventral keel, (3) unmodified
dorsum of penis valve	(1) dorsal ridge, (2) dorsal crest, (3) unmodified
dorsal depression of penis valve	(1) present, (2) absent
penis valve	(1) narrow, (2) usually expanded
volsella	(1) small, (2) normal, (3) enlarged
volsella inner margin	(1) notched medially, (2) not notched
color	(1) orange with green reflections, (2) bright green, blue, or red, (3) largely dark with green tints, (4) brown or dull metallic, (5) dull metallic, (6) orange with dull green reflections
average size	(1) small, (2) medium, (3) large
macrocephalic individuals	(1) never present, (2) sometimes present

Table 3. Coding of augochlorine genera and subgenera for numerical analysis.

Code	Taxon	Code	Taxon
1	Megaloptidia	17	Augochlora s. s.
2	Megommation s. s.	18	Oxystoglossella
3	Megaloptina	19	Mycterochlora
4	Ariphanarthra	20	Megalopta
5	Thectochlora	21	Caenaugochlora s. s.
6	Rhectomia	22	Ctenaugochlora
7	Corynurella	23	Pseudaugochloropsis
8	Rhinocorynura	24	Neocorynura s. s.
9	Corynura s. s.	25	Neocorynuroides
10	Callochlora	26	Temnosoma
11	Halictillus	27	Paroxystoglossa
12	Chlerogas	28	Andinaugochlora
13	Chlerogella	29	Augochloropsis s. s.
14	Ceratalictus	30	Paraugochloropsis
15	Pereirapis	31	Augochlorodes
16	Augochlorella		

TABLE 4. Matrix of Correlation Coefficients among Augochlorine Genera and Subgenera *(Upper Right)*
TABLE 5. Matrix of Distance Coefficients among Augochlorine Genera and Subgenera *(Lower Left)*

O.T.U.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1.	**xxx**	.74	.55	.67	−.07	−.19	−.16	−.08	−.18	−.26	−.27	−.13	.09	−.19	−.19	.02	−.03	−.05	−.12	.08	−.06	−.04	.04	−.23	−.33	−.19	−.17	−.37	−.27	−.23	−.22
2.	0.82	**xxx**	.78	.57	−.10	−.22	−.15	−.11	−.29	−.31	−.30	−.02	.03	−.19	−.24	−.06	−.11	−.13	−.18	.08	−.18	−.13	.12	−.34	−.33	−.07	−.19	−.22	−.06	−.01	.05
3.	1.04	0.71	**xxx**	.54	−.08	−.16	−.16	−.09	−.26	−.23	−.20	−.10	.04	−.13	−.18	−.06	−.13	−.16	−.20	.01	−.19	−.15	.19	−.30	−.31	−.06	−.22	−.12	−.09	−.05	−.03
4.	0.89	0.99	0.98	**xxx**	−.04	−.17	−.04	−.08	−.30	−.29	−.26	.01	.12	−.10	−.18	−.02	−.09	−.11	−.14	.05	−.13	−.07	.16	−.28	−.33	−.13	−.22	−.14	−.16	−.13	−.06
5.	1.42	1.40	1.32	1.30	**xxx**	.13	−.19	.07	−.10	−.01	.05	−.19	−.27	.27	.02	.06	−.22	−.20	−.20	−.06	.02	.05	−.05	−.05	.06	−.10	.21	.03	.12	.12	.11
6.	1.63	1.68	1.55	1.57	1.14	**xxx**	.53	.39	.33	.09	.34	−.35	−.09	−.05	−.20	−.29	−.27	−.31	−.23	−.01	−.22	−.07	−.24	.20	.10	−.10	.11	−.22	−.11	−.07	.10
7.	1.56	1.57	1.51	1.43	1.33	0.94	**xxx**	.44	.09	.00	.15	−.09	.28	−.17	.02	−.11	−.07	−.08	−.22	.05	−.08	−.01	−.17	.04	−.06	−.09	−.13	−.11	−.19	−.20	.02
8.	1.68	1.66	1.60	1.59	1.34	1.29	1.12	**xxx**	.17	.06	.12	−.15	−.09	−.09	−.14	−.24	−.15	−.19	−.14	−.01	−.18	−.15	−.23	.03	−.03	.01	−.06	−.21	−.04	−.03	−.14
9.	1.53	1.58	1.50	1.52	1.20	1.03	1.23	1.31	**xxx**	.77	.70	.00	.07	−.03	−.08	−.23	−.15	−.15	−.15	−.24	−.22	−.21	−.19	.23	.07	−.05	−.08	.21	−.22	−.19	.05
10.	1.68	1.66	1.55	1.59	1.23	1.30	1.35	1.43	0.63	**xxx**	.58	−.02	−.11	.08	−.02	−.15	−.15	−.14	−.12	−.23	−.05	−.17	−.15	.13	.03	.03	−.12	.23	−.17	−.17	.05
11.	1.64	1.65	1.53	1.57	1.18	1.09	1.24	1.39	0.71	0.87	**xxx**	.02	.12	−.19	−.13	−.31	−.21	−.22	−.24	−.27	−.17	−.08	−.18	.25	.15	−.12	−.04	.27	−.04	−.13	.16
12.	1.60	1.49	1.47	1.42	1.48	1.70	1.56	1.58	1.40	1.47	1.45	**xxx**	.44	−.17	−.02	−.10	−.28	−.28	−.24	−.16	.00	.01	.03	.13	.02	.01	−.03	.26	.02	.00	.17
13.	1.63	1.70	1.60	1.50	1.65	1.65	1.38	1.94	1.41	1.67	1.46	1.43	**xxx**	−.03	−.13	−.17	−.14	−.15	−.19	.08	−.10	−.14	−.03	−.14	−.20	.10	−.21	−.05	−.29	−.26	.01
14.	1.38	1.42	1.32	1.29	0.86	1.15	1.28	1.41	1.12	1.16	1.28	1.41	1.52	**xxx**	.45	.56	.05	.09	−.05	−.10	−.07	−.02	−.07	.02	.11	.03	.13	.03	−.14	−.18	−.15
15.	1.41	1.45	1.34	1.34	1.00	1.23	1.19	1.44	1.15	1.21	1.25	1.34	1.45	0.69	**xxx**	.43	.19	.22	.11	−.18	.07	−.06	−.04	.08	.12	−.13	−.06	−.08	−.11	−.14	−.02
16.	1.28	1.31	1.24	1.22	0.94	1.18	1.21	1.44	1.17	1.23	1.29	1.36	1.40	0.60	0.68	**xxx**	.18	.23	.15	−.05	.09	.03	−.02	−.11	.07	−.06	.09	.01	−.18	−.18	−.03
17.	1.55	1.55	1.52	1.49	1.38	1.66	1.43	1.61	1.40	1.47	1.51	1.56	1.89	1.20	1.12	1.09	**xxx**	.88	.67	−.09	.05	−.01	−.03	−.08	.03	−.17	−.16	−.16	−.12	−.11	−.24
18.	1.50	1.51	1.47	1.44	1.29	1.57	1.37	1.58	1.34	1.40	1.45	1.57	1.77	1.10	1.03	0.99	0.47	**xxx**	.53	−.06	.10	.04	.00	−.05	−.03	−.10	−.15	−.11	−.13	−.13	−.23
19.	1.58	1.60	1.56	1.52	1.36	1.52	1.52	1.60	1.40	1.45	1.52	1.61	1.82	1.19	1.16	1.10	0.80	0.92	**xxx**	−.05	.11	.13	.00	−.11	−.01	−.10	.04	−.09	.01	−.02	−.19
20.	1.77	1.65	1.68	1.68	1.63	1.77	1.62	1.74	1.78	1.81	1.84	1.91	1.97	1.66	1.69	1.58	1.75	1.68	1.71	**xxx**	.00	−.13	.11	−.16	−.01	−.06	.03	−.06	.01	.01	−.06
21.	1.51	1.55	1.50	1.46	1.18	1.38	1.38	1.58	1.38	1.35	1.42	1.48	1.59	1.19	1.12	1.07	1.32	1.22	1.27	1.64	**xxx**	.56	.02	.02	.07	−.12	.08	−.03	−.06	−.07	−.05
22.	1.31	1.39	1.34	1.30	1.02	1.17	1.21	1.43	1.23	1.29	1.23	1.31	1.48	1.01	1.03	0.94	1.23	1.13	1.14	1.63	0.78	**xxx**	−.03	−.01	.03	−.12	.04	.11	−.03	−.06	.07
23.	1.55	1.46	1.37	1.40	1.40	1.50	1.58	1.72	1.53	1.55	1.57	1.54	1.46	1.42	1.40	1.35	1.50	1.43	1.48	1.58	1.42	1.35	**xxx**	−.17	−.27	−.05	.07	.09	−.08	−.10	−.06
24.	1.52	1.63	1.54	1.53	1.18	1.12	1.28	1.43	1.08	1.22	1.12	1.39	1.63	1.09	1.06	1.12	1.38	1.29	1.39	1.76	1.25	1.14	1.55	**xxx**	.76	−.21	.21	.15	−.23	−.22	−.01
25.	1.68	1.67	1.59	1.60	1.16	1.29	1.38	1.50	1.23	1.33	1.23	1.48	1.80	1.09	1.08	1.08	1.35	1.33	1.37	1.75	1.26	1.16	1.65	0.63	**xxx**	−.27	.26	.11	−.07	−.07	.06
26.	2.27	2.11	2.06	2.12	1.95	2.10	2.05	2.08	1.98	1.95	2.07	1.83	2.14	1.84	1.88	1.88	2.11	2.03	2.05	2.26	2.04	1.95	2.12	2.10	2.19	**xxx**	−.04	−.16	.18	.16	−.16
27.	1.49	1.45	1.40	1.40	0.94	1.11	1.29	1.41	1.19	1.28	1.23	1.38	1.58	0.95	1.04	0.93	1.34	1.26	1.22	1.56	1.14	1.02	1.31	1.02	1.03	1.91	**xxx**	.08	−.04	−.10	.11
28.	1.47	1.39	1.27	1.29	0.97	1.21	1.21	1.42	0.96	1.02	0.99	1.11	1.41	0.93	0.98	0.90	1.27	1.17	1.23	1.55	1.13	0.91	1.25	1.01	1.07	1.93	0.94	**xxx**	−.03	−.04	.16
29.	1.73	1.54	1.51	1.54	1.21	1.46	1.50	1.55	1.48	1.50	1.49	1.48	1.84	1.34	1.32	1.31	1.50	1.46	1.41	1.67	1.41	1.27	1.54	1.50	1.44	1.86	1.30	1.23	**xxx**	.97	.03
30.	1.68	1.49	1.47	1.52	1.19	1.43	1.51	1.52	1.44	1.48	1.46	1.49	1.81	1.32	1.31	1.28	1.48	1.43	1.41	1.66	1.40	1.26	1.54	1.47	1.42	1.86	1.31	1.20	0.25	**xxx**	.01
31.	1.48	1.31	1.29	1.30	0.99	1.05	1.21	1.45	1.11	1.19	1.11	1.26	1.34	1.07	1.01	0.98	1.38	1.30	1.35	1.62	1.21	1.00	1.40	1.15	1.16	1.99	0.99	0.90	1.26	1.24	**xxx**

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